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MASTICATION IN THE FREELY MOVING RAT

by



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A THESIS

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Mastication in the Freely-Moving Rat", submitted by Sue Corley Peyton in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

ABSTRACT

A head assembly for rats is described by means of which afferent input and efferent output of the masticatory system may be recorded simultaneously during normal chewing. The assembly can be worn by the animal for several months without discomfort. It consists of 1) chronic multiunit stainless steel electrodes placed in the mesencephalic nucleus of the trigeminal nerve (Mes V) and 2) from one to three fine silver wire bipolar EMG electrodes led subcutaneously from the head pedestal to masseter, temporalis, and digastric muscles. In addition, several animals were fitted with a jaw movement transducer along with bipolar EMG electrodes in masseter to show relationships between actual jaw position and EMG activity.

After fasting for 24 hours, freely moving animals were allowed to eat one of several normal foods while observed in a clear recording cage. The overhead recording leads did not restrict normal movement in any way.

Masseter, temporalis, and Mes V are each active during the same single period of the chewing cycle. The digastric muscle, a jaw depressor, has two periods of activity. One of these is during the opening phase of the chewing cycle, but the other is during the closing phase, concurrent with Mes V and the jaw elevators.

Normal molarization involves from 25 to 35 cycles. Cycle times vary with load; thus chewing of bread (6 Hz) is faster than or large or small pellets (5 Hz) and pudding is eaten twice as fast as are pellets (10 Hz). Closing and occlusion periods were

very brief for large and small pellets, while opening lasted over 70% of the cycle. For bread, both opening and closing phases lasted about 40% of the cycle. A silent period was seen in Mes V, temporalis, and masseter.

All Mes V activity recorded through the chronic multi-unit electrodes during normal chewing occurred during jaw closure. This activity was found to be largely composed of muscle spindle activity. Thus the spindles were active while the muscles were being unloaded. Since the reflex theory of mastication requires spindle activity when the jaw elevator muscles are stretched, the reflex theory of mastication is disconfirmed.

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I. INTRODUCTION

Mastication, or the chewing of food, is one of the basic rhythmic muscular activities in mammals. It involves the coordinated movements of mandible and tongue, along with other oral and perioral structures. The function of mastication is conversion of large pieces of food into small particles which are more easily swallowed and digested. For most animals, this requires some form of biting or tearing from a large piece of food, incision and the positioning of the bolus in the mouth before the grinding or molarization stage can begin. The process also results in release of salivary and gastric secretions through appreciation of flavor during chewing (Anderson, 1968). "Oral satisfaction" has been important for such diverse psychological theories of human behaviour as those of Freud and of the behaviourists. These psychologists have considered eating to be a primary drive and therefore it has been studied extensively with respect to problems of motivation and learning. In fact, most of Skinner's work on operant conditioning is based on the willingness of the subject to learn or perform work for food (Chaplin and Krawiec, 1960). The emotional satisfaction obtained from having something in the mouth is considered a primary factor in the problems of obesity control and breaking the habit of cigarette smoking.

The same basic physiological apparatus involved in mastication is also used for vocalization. The shift from use of the jaws for prehension to use in talking and the consequent change in control mechanisms of the masticatory muscles have been credited (blamed) by

Dubru! (1960) for the evolution of man from the ape. Clearly, study of the masticatory process and its control has many important implications. Nevertheless, an understanding of the active chewing process itself is the primary goal.

II. REVIEW OF THE LITERATURE

A. Anatomy

i) *The basic components and receptors of the system.*

The masticatory system is fairly complex. The teeth are located in the maxilla and mandible, the basic lever system connected by the temporomandibular joint (TMJ). Teeth and TMJ are supplied with special joint, pressure and pain receptors. The joint is opened and closed by two basic sets of muscles. The jaw openers include lateral pterygoid, digastric, mylohyoid and geniohyoid muscles (the suprahyoid muscles) with some help from the infrahyoid group to stabilize the hyoid bone. The jaw closing muscles or elevators include masseter, temporalis and medial pterygoid. These are the antigravity muscles and are well supplied with proprioceptors. (Presence of proprioceptors in the jaw depressor group is much less clear.) Finally, the tongue, cheeks, lips and hard and soft palates with their associated mucosa are involved in containing and positioning the food bolus (Huber, 1964; Kawamura, 1964).

In man, the temporomandibular joint allows a great deal of freedom of movement, like other synovial joints. It has a loose capsule and freely movable meniscus. To fully open the mouth, the lateral pterygoid muscle contracts; this pulls the head of the mandible and the meniscus forward, balancing the head of the mandible on the articular eminence to allow biting. Temporalis is the largest muscle (45% of the total muscle mass), followed by masseter (28%), medial pterygoid (11%) and lateral pterygoid (15%) (Smith and Marcarian,

1967). The TMJ of cats is almost a hinge joint, severely limited in lateral deviation and protraction. Temporalis is the largest muscle, as in man, weighing 79% of the total weight of jaw elevators. Masseter comprises 18%, medial pterygoid 4%, and the lateral pterygoid is a minimal 0.3% (Becht, 1953; Shumacher, 1961; Smith and Marcarian, 1967). Like man, the rat TMJ permits a large degree of freedom of movement. In gnawing, the jaw is shifted forward to place the lower incisors opposite the incisors of the maxilla. An additional joint is present, the intramandibular, since the two halves of the rat mandible are not fused at the symphysis. Masseter is the largest of the masticatory muscles (66%), while temporalis is less than half as large (26%). Medial pterygoid and lateral pterygoid represent 0.08% and 0.03% of the elevator muscle mass, respectively (Becht, 1953; Hiimäe, 1967; Smith and Marcarian, 1967).

Most physiologists, especially those working on mastication, will admit that the animal they would like to study is man. However, he is unsuitable for many types of experiments due to ethical considerations, so another choice must be made.

Human mastication occurs in three planes: vertical, horizontal and transverse. The human diet is omnivorous, rather than strictly carnivorous. The rat chews in all three planes, while cats and dogs chew mainly in the vertical plane. The rat also has a more varied diet than do the carnivorous cats and dogs. For these reasons, it seems desirable to use the rat for experimental studies of active chewing. Where the information is available the rat will be discussed, since that animal was used for this study. Rabbits, cats

and dogs also have been used in many of the studies reported below. The picture of mastication which emerges is a composite, incomplete for *any* particular subject.

Based on an analysis of fiber content, Hiemäe (1967) divides the rat masticatory muscles into a tonic or predominantly red muscle fiber group and a phasic or predominantly white fiber group. Anterior temporal, deep masseter, and lateral pterygoid have the highest red fiber content. She suggests that the two large muscles stabilize the mandible, while the small lateral pterygoid would control the position of the mandibular condyle, confirming Smith and Marcarian (1967).

Although some dark fibers were present in all of the masticatory muscles, the lowest count was found in superficial masseter and posterior temporal. She believes that while all of the masticatory muscles produce movement, these two would be largely responsible for the rapid horizontal movements. An analysis of the effective lines of force in the masticatory muscles, along with the potential magnitude of force from them, was used to divide the rat's muscles into two more groups. First, "those with substantial force available in all directions but with a relatively small amplitude of movement", and second, "those capable of moving the mandible through considerable distances but without a great deal of power" (Hiemäe, 1967). Anterior temporal, deep masseter, and internal pterygoid made up the first group, while superficial masseter and posterior temporal muscles comprised the second. Stabilization of the joint is considered to be an especially important function for rats due to the

absence of a strongly encapsulated TMJ.

The muscles of mastication, like all the muscles of the body, are equipped with a variety of specialized nerve endings, including motor end plates, Golgi tendon organs, and the various afferent and efferent fibers associated with the muscle spindles. Karlsen (1965) found that the end plates of the α motoneurons in these muscles are arranged in a single zone of innervation, located halfway between the ends of the muscle and almost perpendicular to the direction of the muscle fibers. The fibers themselves are continuous from origin to insertion. Although no one seems to have looked for Golgi tendon organs in rat masticatory muscles, they were found in cat temporalis and masseter by Szentagothai (1948). Several people have looked for muscle spindles in the rat masticatory muscles. Smith and Marcarian (1967) found them in temporalis, masseter and medial pterygoid, but not in lateral pterygoid. No numbers were given. The more quantitative study of Karlsen (1965) discovered 130 spindles in masseter, 46 in temporalis, 16 in medial pterygoid and none in lateral pterygoid (counts were made in serial sections from a single muscle of one animal and therefore must be regarded in relative rather than absolute terms. However, sixteen samples of each muscle type were examined for presence or absence of spindles.) He notes that only six spindles were found in superficial masseter, while Freimann (1954) had found 118 spindles in the superficial portion of human masseter and only 42 in the deep portion. In all of the rat muscles having them, spindles were concentrated in the medial portion of the muscle.

Karlsen (1965) found both chain and bag intrafusal fibers in the rat spindles. From five to seven intrafusal fibers are found, of which one to three are bag fibers. This contrasts with the two bag and two chain fibers found in rat rectus femoris and soleus by Barker and Hunt (1964) and in the plantar lumbrical muscles by Porayko and Smith (1968). In fact, Karlsen found a few spindles with ten to twelve intrafusal fibers. Many spindles found at different levels in the transverse planes shared a common capsule, thus forming a sort of "giant" spindle. He found primary or annulospiral endings on both chain and bag fibers. These Ia fibers exhibited branching both inside and outside the capsule, in contrast to the comparative rarity of Ia branching found by Barker (1962). Secondary endings were present in some, but not all, spindles, especially on the nuclear chain fibers. "Structures similar to extrafusal motor end plates" and arising from relatively small fibers were seen towards the polar region of jaw muscle intrafusal fibers. Some flowerspray endings were also found, so it appears fairly likely that these particular rat spindles have both the spiral and flowerspray group II terminations, like the cat (Granit, 1970). In addition, small irregularly distributed dots, associated with small nerve fibers, were seen in all but the equatorial region. Perhaps these and the plate endings correspond to the two types of motor nerve terminals (i.e., γ motoneuron) found by Porayko and Smith.

It is generally felt that the jaw opening muscles do not have spindles. Voss (1956) found none in human mylohyoid, geniohyoid,

stylohyoid or posterior belly of digastric, but reports six in the anterior belly of digastric (less than 2/g of muscle). Szentagothai (1948) found no degeneration in nerves to anterior digastric, mylohyoid and tensor muscles after cutting the mesencephalic tract of the trigeminal nerve in cats. Thomas and Dmytruk (1970) found no spindles in rat digastric, though Shehata (1971), after observing ten rat digastric muscles, found a total of *one* spindle in anterior digastric. It consisted of one nuclear chain and three nuclear bag intrafusal fibers. He was unable to see any spiral endings (or any other endings). Shehata also looked at the motor end plates of the extrafusal fibers in digastric. Like Karlsen, he found only one end plate on a single motor fiber.

The teeth are provided with receptive organs both within and around the periphery. These intradental and periodontal receptors have been studied extensively in many animals, including the human (Anderson, Hannam and Matthews, 1970). However, information on the rat is almost non-existent. Sheinin and Light (1969) found both very fine caliber (1 - 2 μ) and thicker myelinated fibers in the spiral portion of the pulp in Sprague-Dawley rats. They believe the fine fibers may be involved in circulatory regulation. In general, intradental receptors seem to receive pain information. Evoked potentials produced by electrical stimulation of tooth pulp in cats (Anderson *et al.*, 1970) have been recorded from spinal nucleus V and traced into midbrain, thalamus, and cortex. Both rapidly adapting and slowly adapting mechanoreceptors are present in the periodontal ligament (Anderson *et al.*, 1970; Beaudreau and

Jerge, 1968; Jerge, 1963a) with the slowly adapting units being most prevalent (Ness, 1954). As with intradental receptors, both large myelinated fibers and small fibers which may or may not be myelinated are found along with a variety of terminal forms (Anderson *et al.*, 1970). The rabbit incisor, a continuously erupting tooth like the rat's, will respond to a force as low as 1 g, though some single units might require up to 19 g. The rabbit periodontal receptors exhibit directional sensitivity (Ness, 1954) like that found for cat (Pfaffmann, 1939a), though the tooth as a whole exhibits no directional sensitivity. Pfaffman (1939b) found that the entire inferior dental nerve could "follow" vibratory frequencies of over 1,000 Hz, but individual units could follow considerably less, ranging from 75 to 520 Hz. These receptors have cell bodies in both the semilunar ganglion (Beaudreau and Jerge, 1963) and mesencephalic nucleus of the trigeminal nerve (Mes V; Corbin and Harrison, 1940; Dault and Smith, 1969; Jerge, 1963a; Kidokoro, 1968a; Smith and Marcarian, 1968). The central processes of the semilunar ganglion tooth receptors usually divide, terminating in the sensory trigeminal nucleus (Sensory V) and also spinal V (Anderson *et al.*, 1970; Kawamura and Nishiyama, 1966). Mes V cells may synapse in the supratrigeminal nucleus before making their known disynaptic connection with the motoneurons of the motor nucleus of the trigeminal nerve (Motor V; Jerge, 1964). The nuclei of the trigeminal system, along with their major reflex connections, are illustrated in Figure 1, from Jerge (1964).

The rat TMJ has been shown to contain "specialized

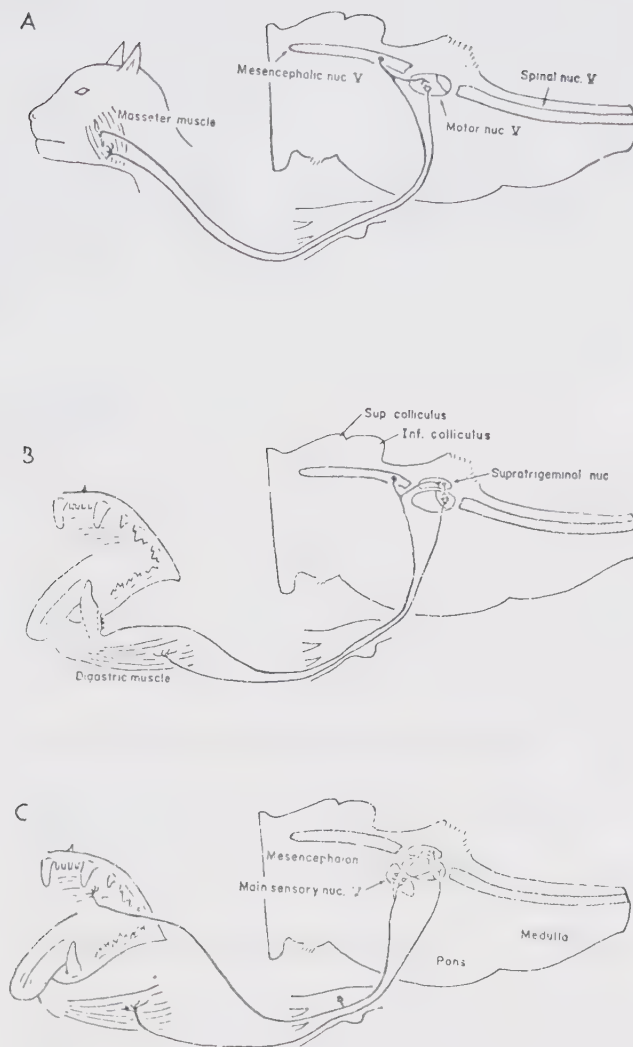


Figure 1. Basic reflexes of mastication. "Jaw reflexes interact to produce cyclic jaw movements. A. The myotatic reflex of the jaw elevator muscles. This is a monosynaptic reflex of mesencephalic nucleus cells with motoneurons of the trigeminal motor nucleus. B. and C., the probable pathways for the jaw opening reflex. Digastric muscle motoneurons can be activated by way of cells of the mesencephalic and supratrigeminal nuclei. B. The receptors of the mesencephalic nucleus cells lie in the periodontal ligament, and an interneuron of the supratrigeminal nucleus makes the reflex polysynaptic. An alternate method of activation is by way of primary cells of the Gasserian ganglion (C) which project to the main sensory nucleus. The second neuron might project to the motor nucleus directly or to interneurons of a more complicated reflex pathway. C. The first neuron projects centrally from a receptor in the hard palate." From Jerge (1964).

encapsulated endbulbs", presumably attached to the nerves traced to its central articular area (Bernick, 1962). Franks (1965) observed three types of nerve endings in the TMJ capsule: free, Pacinian corpuscles and complex noncapsulated nerve endings. His study was done on cats, rabbits, guinea pigs and rats.

ii) *The trigeminal system.*

It could be said that the study of neural control of mastication is the study of the trigeminal nerve, its associated nuclei and the upper level control systems acting upon them. With the exception of stylohyoid, posterior belly of the digastric, and geniohyoid, supplied by the facial and hypoglossal nerves, all of the jaw muscles are innervated by branches of the mandibular division of the trigeminal nerve (Gray, 1959; Huber, 1954). Sensory nerves from the TMJ travel in the auriculotemporal and masseteric branches of the mandibular trigeminal division (Gray, 1959), while those from upper and lower teeth and gingiva proceed by the superior and inferior alveolar (dental) nerves, branches of maxillary and mandibular divisions of the fifth nerve. In addition, the maxillary division receives a branch from the mucous membrane of the palate. Thus only the tongue, of the major components of the masticatory system, is not under direct control of the trigeminal system, and there are well-established reciprocal reflexes to coordinate activity in its hypoglossal nerve with the trigeminal system.

The trigeminal nerve consists of the sensory root, divided into ophthalmic, maxillary and mandibular divisions at the

semilunar (Gasserian) ganglion, and the motor root, which joins the main nerve just distal to the semilunar ganglion. This root is perhaps misnamed "motor", since it contains the afferent fibers to Mes V along with the motoneurons to the masticatory muscles.

Sherrington (1917) found three masticatory reflexes: jaw opening followed by rebound closure, jaw closure which was maintained, and jaw jerk (response to stretching the jaw elevators by quickly opening the mouth). These are all mediated by the trigeminal complex. As early as 1896, Cajal had seen collaterals of Mes V proceeding to Motor V. Corbin and Harrison (1940) recorded potentials in Mes V root in response to jaw opening and to blunt pressure on the homolateral teeth, gums and hard palate. Lesion of Mes V root just rostral to Motor V abolished the "jaw jerk" response. Electrical stimulation of Mes V produced contraction of the masticatory muscles while stimulation of Sensory V and Spinal V produced jaw opening (Harrison and Corbin, 1942). Thus, Sensory V, Motor V, Mes V and Spinal V quickly enter any discussion of mastication.

Sensory V units respond to noxious stimuli of the mouth and lips (Kawamura, 1964), painful pulp stimulation (Dunker 1967) and pressure on teeth (Kawamura and Nishiyama, 1966). Stimulation of teeth or gums results in jaw opening (Hannam and Matthews, 1968, 1969; Hannam *et al.*, 1970; Jerge, 1963a; Kawamura, 1964; Kidokoro, 1968a; Sherrington, 1917) through inhibition of jaw elevators. Although Kidokoro believes that tooth receptors function reflexly in normal control of mastication, evidence

presented by Anderson *et al.* (1970) argues in favor of a purely protective function. The latter authors point out the similarity between dental mechanoreceptors and Type II skin receptors.

Beaudreau, Daugherty and Masland (1969) have proposed that periodontal receptors may perform for the masticatory system some of the functions of Golgi tendon organs in other somatic muscles.

Sensory V units also respond to movement at the temporomandibular joint (TMJ) (Majima and Kawamura, 1965). When the condyle was rotated in the jaw opening direction, masseteric motoneurons in Motor V were activated while condylar rotation in the jaw closing direction produced inhibition; digastric motoneurons were facilitated by closing and inhibited by opening.

In general, Sensory V has more fibers from the mandibular division than from maxillary and ophthalmic (Darian-Smith, 1966; Kimmel, Lesavoy and Yeston, 1967). The neurons from the oral cavity are found in the medial portion of Sensory V, where each point is represented by a column of cells oriented in the rostro-caudal direction; these columns extend throughout Spinal V, with the exception of nucleus interpositus (Eisenmann, Landgren and Novin, 1963; Kruger and Michel, 1962). The complex of Sensory V and Spinal V nucleus oralis deals with tactile perception and is analogous to the medial lemniscus (Mountcastle and Darian-Smith, 1968).

Darian-Smith (1966) reviews this system and discusses its relationship with higher brain centers. A discussion of fine structure of Sensory V for rat and cat is presented in Gobel and Dubner (1969). By stimulating the inferior dental nerve of cats with single shocks,

Wyrwicka and Chase (1969) have recorded evoked potentials in lateral hypothalamus, preoptic area, the ventral tegmentum, and nucleus ventralis posteromedialis, the thalamic nucleus which is a relay for taste. Stimulus-bound feeding has been obtained from all of these areas. Electrolytic and surgical lesions, in cats and monkeys, respectively, of Sensory V and the supra-trigeminal nucleus have produced evidence of two major ascending tracts, that is, ipsilateral and contralateral projections to the posteromedial ventral nucleus of the thalamus (confirming Wyrwicka and Chase); in addition, an ipsilateral tract was found proceeding to Spinal V (as would be expected from all of the above!). Fibers from the sensory root of the trigeminal nerve have been traced through Sensory V to the dorsolateral reticular formation, and fibers of the mandibular branch were traced to the medial region of nucleus solitarius (Kimmel, Lesavoy and Yeston, 1967). Unit cell activity was recorded in the cat pontine reticular formation in response to touch on the face; no units responded to proprioceptive stimulation (Langlois and Lamarche, 1962).

The motoneurons involved in mastication generally resemble those of the spinal cord. But they lack collaterals (Cajal, 1909) like those in the spinal cord which produce recurrent inhibition through Renshaw cells (Doty, 1968). This has been confirmed physiologically by Porter (1965) for hypoglossal motoneurons. Both trigeminal and hypoglossal motoneurons (mns) receive direct peripheral afferent input (from Mes V; Szentagothai, 1948).

Central afferent inputs come from the reticular formation (Jerge, 1963a; King *et al.*, 1955), nucleus solitarius, pyramidal tract, and probably other sources also (Doty, 1968).

Motor V is arranged topographically (Szentagothai, 1949; Vedral and Matzke, 1967), with those muscles having origin at higher levels on the head (masseter, temporalis) localized in the ventral part of the nucleus, while lateral and medial pterygoid are located in the dorsal nucleus. This arrangement is also found in the facial nerve and, according to Szentagothai, corresponds to sensory representation of the face in Spinal V, with areas supplied by the mandibular division being found dorsally and those supplied by ophthalmic division in the ventral part. Muscles lying near the mouth (masseter, pterygoids) are found in the anterior nucleus, those further away (temporalis, anterior digastric) closer to the posterior pole. It is not completely clear how the antero-dorsal localization of mylohyoid fits this scheme.

Increased frequency in a Motor V unit induced by stretching a jaw muscle is inhibited by stretch of the antagonistic or symmetrical muscle (that is, increased frequency caused by masseter stretch would be abolished and decreased below the background level by either stretch of ipsilateral digastric or contralateral masseter). Stretch of the synergistic muscle (temporalis in the example) results in an even greater frequency of discharge in the unit being studied than that found by stretch of the original muscle (Kawamura, 1964; Kawamura, Funakoshi and Takata, 1960).

Thus, a muscle receptor in Mes V not only communicates with the same muscle mn in Motor V but also sends collaterals to areas of other muscles in Motor V, allowing for facilitation and inhibition between muscles. Mes V units fire only on stretch of an ipsilateral elevator muscle, subsequent stretch of either a jaw depressor or the contralateral elevator muscle having no effect.

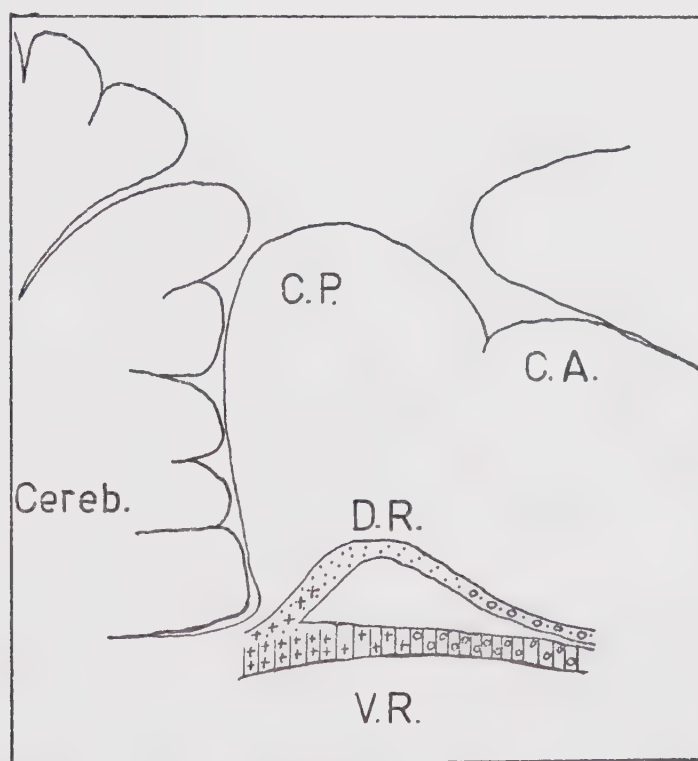
Mes V displays some definite interspecies differences. There is a consistent increase in cell number relative to the size of the animal, up to the mammalian level. In both birds and mammals, number of Mes V cells is related to both size of the animal and complexity of the jaw musculature (Dubrul, 1960). So the rat has more Mes V cells than the cat (Hinrichson and Larramendi, 1969), even though it is much smaller in size. Cell distributions also differed somewhat: in the cat there were noticeable rostral and caudal concentrations, but not nearly so marked as in the mouse and rat; mouse showed a pronounced caudal cell concentration; in the rat 50% of all cells were within 450 μ of the caudal termination of the nucleus. This may be related to the relative amount of "clustering" found in Mes V nuclei, the caudal area having more and larger cell clusters. These authors found no provision for a γ system in the mouse Mes V since the fiber distribution was unimodal. Perhaps the mouse uses Barker's β fiber system (1966). In 1969, Brightman and Reese reported "gap junctions" between Mes V cell bodies. This was confirmed by Hinrichson and Larramendi (1970) who also found axosomatic synapses on these cells. Although the cells were studded with spinous processes, all synapses were





directly on the soma. They raise the point that modification of sensory input might be occurring at the cell body rather than at the presynaptic terminal. Such synapses contained either round or ovoid vesicles, a possible indication that both facilitatory and inhibitory transmitters were present. Hinrichson (1970) presents some evidence that the gap junctions allow electrotonic coupling. Quite strong evidence for electrotonic coupling between Mes V cells in the rat is presented by Baker and Llinás (1971). This may be important for coordination in the masticatory system.

In the rat, Mes V begins caudal to the posterior commissure, just at the level of the oculomotor nucleus, and proceeds posteriorly to just beyond motor V. The size of the nucleus slowly increases going posteriorly, proceeding to a point beyond the trochlear nucleus. Between the decussation of the trochlear nucleus and the beginning of Motor V are located the largest number of Mes V cells. Thereafter they decrease rapidly (Hinrichson and Larramendi, 1969; Weinberg, 1928). The cell bodies forming the nucleus lie between the central gray and the axons of the Mes V tract. In the midbrain these cells are lateral to the cerebral aqueduct, and approximately on the same level, just lateral to the periventricular gray. It gradually begins to extend below the level of the aqueduct, until by the level of Motor V, the dorsal limit of Mes V is the ventral limit of the cerebral aqueduct. The nucleus is thus a long column of cells ranging from 3.5 to 3.8 mm long (Hinrichson and Larramendi, 1969; Weinberg, 1928) traversing the entire midbrain along the cerebral

aqueduct and continuing just below the floor of the fourth ventricle to end at the level of the pons just posterior to Motor V.

Mes V contains afferents from muscle spindles of the masticatory muscles and from periodontal mechanoreceptors of single teeth or groups of teeth and the contiguous gingiva (Cooper, Daniel and Whitteridge, 1953; Corbin, 1940; Corbin and Harrison, 1940; Jerge, 1963a; Szentagothai, 1948; Taylor and Davey, 1968). Spindle units seem to be distributed uniformly along the length of the nucleus in cat (Jerge, 1963a) while tooth receptors may be located more caudally (Corbin and Harrison, 1940; Jerge, 1963a).



	Internal pterygoid
	External pterygoid
	Temporalis
	Masseter

C.A.	colliculus anterior
C.P.	colliculus posterior
D.R.	dorsal ramus of Mes V
V.R.	ventral ramus of Mes V

Figure 2. Somatotopic localization in Mes V of fibers from masticatory muscles. From Cupedo (1970).

Cupedo (1970) found a somatotopic localization of fibers from masticatory muscles in the rat Mes V root. The nerves to masseter, deep temporalis, medial (internal) pterygoid, lateral (external) pterygoid, and combinations of them were sectioned; the distal segments were removed, and degeneration of the axons was traced after sacrifice of the animals. There was a dorsal-ventral division of the Mes V root, as illustrated above. A single group of cells was found both anterior and posterior to the section illustrated. Temporalis cells are located more rostrally while masseter is more caudal. Very few fibers from lateral (external) pterygoid were found, in spite of the implication of the diagram. No spindles have been found in either intrinsic or extrinsic muscles of the tongue (Blom, 1960). Smith and Marcarian report a bimodal distribution of locations along Mes V where evoked potentials have been recorded in response to pulling on the tongue. (Incidentally, Smith, Marcarian and Niemer, 1967, also report recording evoked potentials in Mes V after stretching lateral pterygoid, known to be without spindles.) No location has been found so far for cell bodies of group II spindle afferents (Smith, Marcarian and Niemer, 1967).

Location of Golgi tendon organ (Ib) fibers is also in question. Hufschmidt and Spuler (1962) assume they are located in Sensory V, but a later study (Smith *et al.*, 1967) points out that, with the exception of Szentagothai's work (1948), no studies of either anatomy or physiology of the Golgi tendon organs have been made. Szentagothai was unable to find any degeneration in Ib

fibers after making extensive lesions in Mes V. He did report tendon organs in masseter and temporalis of cat. Jerge (1963a) found no evidence of Ib cells in Mes V, while Beaudreau and Jerge (1968) were unable to locate them in Sensory V. However, a more recent paper by Smith (1969) seems to demonstrate potentials from Ib fibers in Mes V of cat. Stimulation of masseter produced a silent period in the "spontaneous" activity (that is, more accurately, response of spindles to pull of gravity on jaw of cat) of Mes V; during this period, at about 40% of maximum tension of the muscle, four to eleven single unit potentials were recorded during isometric muscle contraction. Taylor and Davey (1968) were able to record from three such units in the course of twenty-one experiments.

Both afferent and efferent fibers of the masseteric nerve are smaller than those of spinal nerves; the largest fibers found are 12 μ diameter, and only 1% are that big. The large fibers are probably Ia, even though not in the 13 to 22 μ range of spinal Ia's (Smith *et al.*, 1968). These authors believe that Mes V serves as a bilateral integrator of masticatory activity. The masseteric nerve was stimulated and evoked potentials were recorded from ipsilateral and contralateral Mes V and contralateral masseter nerve. Similarly, Mes V was stimulated and the evoked potentials were recorded from contralateral Mes V and masseteric nerve. About half of the masseteric fibers to the ipsilateral nerve project directly and the other half project by way of a synapse. The same was true of the contralateral nucleus. Yet potentials recorded

from ipsilateral Mes V after stimulating contralateral Mes V showed a direct internuclear path. Evoked potentials recorded in one nerve from stimulation of the other always had at least one intervening synapse. They also found direct projections from the masseteric nerve to contralateral Motor V. Thus, unilateral stimulation of either tendon receptors or muscle spindles could activate the masticatory muscles bilaterally. These findings have been confirmed by Thomas (1972) for the rat. Neither Corbin and Harrison (1940) nor Cupedo (1970) found evidence for such contralateral fibers. But an early study by Lewy, Groff and Grant (1938) stated that many Mes V fibers cross to the opposite side. Also, Dault and Smith (1969) sectioned various branches of the trigeminal nerve in cats. For example, unilateral section of the masseter nerve resulted in chromatolysis of 18% of the cells in the ipsilateral Mes V root and of 9.7% of cells in the contralateral Mes V root. Similar results were found for temporalis. In addition, unilateral section of lingual, inferior alveolar, and hypoglossal nerves produced chromatolysis in both ipsilateral and contralateral Mes V roots.

B. *Jaw Reflexes and Neural Pathways*

Using the decerebrate preparation, Sherrington (1917) found three basic reflexes in the masticatory system: jaw closing, in conjunction with swallowing when fluid was placed in the mouth or when the top of the tongue was touched with a feather; jaw opening, from blunt pressure stimulation of gingiva bordering

teeth in either jaw or the front of the hard palate, also pressure on a tooth crown; and the jaw jerk or stretch reflex. The jaw remained closed after jaw closing and jaw jerk reflexes, but jaw opening was quickly followed by a rebound closure after stimulation was stopped. The digastric muscle was responsible for this opening and he postulated concurrent reflex central inhibition of the anti-gravity muscles. The reflex was ipsilateral, since tooth stimulation after splitting of the mandibular symphysis caused opening and rebound closure only on the same side of the jaw that had been stimulated. The reflex theory of mastication states that although movement begins voluntarily by seizing food, the pressure caused brings about opening, followed by rebound closure and renewed stimulation producing opening again, so that rhythmic chewing would be maintained so long as food was able to produce stimulation. Sherrington may not have been so dogmatically convinced of peripheral control of cyclic movements as this theory implies, however, for Lundberg (1968) quotes the following from Liddell and Sherrington (1924) on stepping: "It is, however, rather as an adjuvant to and accessorially adjusting the fundamental phasic movements of the step than as actually producing them, that the stretch reflex must be regarded ... " (note also Granit's comment (1968) about the luck of choosing a decerebrate preparation). Sherrington also found a considerable cortical projection of the jaw which controlled contralateral muscles.

The monosynaptic stretch reflex of the trigeminal nerve has long been established (Harrison and Corbin, 1942; Hugelin and

Bonvallet, 1956; McIntyre, 1951; Szentagothai, 1948). Muscle spindles of the jaw elevators excite the homonymous mns in Motor V through the Ia fibers which have their cell bodies in Mes V. Collaterals of these Ia fibers were traced to the ipsilateral motor nuclei of the infrahyoid muscles, that is, to the caudal part of the hypoglossal nucleus and the ventral horn on C1 and C2. It is interesting that Szentagothai found not only the large Ia fibers, but also "medium-sized fibers, which terminate in muscle spindles as flower-spray endings" to be involved in the "two-neuron reflexes". The jaw opening reflex (Sherrington, 1917) is produced "by pressure stimulation of the gingivae in the anterior part of the mouth, the incisors or canine teeth, or the anterior part of the hard palate" (Jerge, 1964). The two forms of this reflex, along with the monosynaptic stretch reflex, are shown in Figure 1 from Jerge (1964, see p. 10). In 1B, a periodontal receptor with cell body in Mes V is shown synapsing first in the supratrigeminal nucleus and then with mns in Motor V to form a disynaptic path. 1C shows a periodontal receptor with cell body in the semilunar ganglion which projects to Sensory V. From there, a disynaptic pathway is completed to Motor V or this connection is made through the supratrigeminal nucleus. In each case, a minimum of two synapses is involved.

Kidokoro *et al.* (1968a, b) discuss the problem of reflex coordination of activity between masseteric and digastric mns. That the mechanism must be somewhat different from reciprocal control in the spinal cord is clear, since the digastric has no

muscle spindles. Stimulation of the inferior dental nerve produces contraction of digastric via a disynaptic pathway while the masseter is inhibited. They consider it likely that afferent collaterals of the inferior dental nerve activate two classes of interneurons, facilitatory to digastric and inhibitory to masseter. Such interneurons appear to be located in the nucleus supratrigeminalis, dorsolateral to Motor V. The supratrigeminal nucleus had been studied earlier by Jerge (1963b) who believed that it fulfilled criteria for interneurons involved in trigeminal reflexes because 1) its neurons were separable from Sensory V neurons by morphological and degeneration studies, 2) it is next to Motor V, separating it from the two afferent sources, Sensory V and Mes V, and 3) its responses fit those found for spinal interneurons. Jaw movement or pressure in the intra-oral field produced facilitation and inhibition of its units; such oppositely reacting units could be found next to each other. Response to pressure stimulation was localized in the caudal part of the nucleus next to the area of Motor V where the digastric mns are found; of course, pressure on teeth results in the jaw opening. Takata and Kawamura (1970) found that all of the supratrigeminal neurons show background activity, increased by deformation of spindles in the jaw closing muscles. In that study, most cells responded only to masseter and others only to temporalis. They were unaffected by stretch of digastric, even though the mns to masseter were inhibited. Such an interneuronal group might provide the location for an oscillator mechanism like that proposed by Jankowska *et al.* (1967) for reciprocal

excitation of flexors and extensors in the spinal cord. Porter (1967) located a group of interneurons for the hypoglossal nucleus in the vicinity of Spinal V or the dorsolateral reticular formation. However, he did no histology. Sumi (1970), also discussing possible interneuronal sites for the cortico-hypoglossal pathway, thought that possible areas included the "mesencephalic tegmental nucleus", that next to Spinal V, or an area in the reticular formation of the lower brain stem.

The importance of the mesencephalon for feeding behaviour has often been discussed. Chewing can be obtained by stimulating the mesencephalic reticular formation according to Kawamura (1960a, b) and Lund and Dellow (1971), while stimulating the substantia nigra might result in tonic closure. Lyon (1966) found that various mesencephalic lesions caused permanent feeding loss, though his results included disruption of Mes V tract. Parker and Feldman (1967) produced feeding losses with small bilateral lesions in the mid-reticular formation between the red nucleus and cerebral aqueduct in the dorsoventral axis. Blatt and Lyon (1968) used assymetric bilateral lesions, one of which was always in the tegmentum dorsolateral to the red nucleus. They suggest the existence of two important pathways, with degree of feeding loss being less severe if both paths were disrupted unilaterally. The paths were 1) a descending route from the basal ganglia or neocortex, and 2) an ascending path of the reticular formation which goes ventrolaterally to the periaqueductal gray in the midbrain, then descends to the zona incerta and fields of Forel in the caudal hypothalamus.

Lyon *et al.* (1968) added the interesting information that feeding deficits did not appear to be related to destruction of posterior lateral thalamus, periaqueductal gray, *mesencephalic root of V*, or descending tectal projections.

Although Ferrier found reflex jaw opening in response to cortical stimulation of cats in 1876, Rioch (1934) was the first to include such stimulation in a theory of mastication. She modified Sherrington's hypothesis by introducing subcortical centers for jaw opening and jaw closing, which were reciprocally influenced by proprioceptive stimuli. Stimulation of the cortex initiates the cycle, stimulating jaw openers (through the jaw opening center?) and inhibiting jaw closers. When the jaw closes, proprioceptive stimulation ceases and the jaw closers relax while the openers contract, either because of cortical or subcortical excitation. No location for the opening and closing centers was suggested. Kawamura, however, has given some physiological evidence for opening and closing centers (Kawamura and Tsukamoto, 1960a, b). Using rabbits, he found that cortical stimulation of the jaw area (rostral to area insularis and lateral to area postcentralis) produced single jaw closing at low frequencies and high threshold, rhythmic chewing of 4.5 to 5.75 Hz at higher frequencies and low threshold. These movements were predominantly opening in nature. Similar results were obtained for the internal capsule, subthalamus, and deep parts of the mesencephalic reticular formation (Mes RF). Single unilateral shocks to these areas produced strong EMG reaction in the digastric while having no effect on masseter. This cortico-

fugal path had an intercalary center probably located in the sub-thalamic region and a possible decussation in the Mes RF. A second pathway was traced from the lateral amygdaloid nucleus through the dorsal Mes RF to the motor nucleus; this path produced EMG activity only in masseter but had a considerably longer latency than the corticofugal path. Stimulation of the amygdala resulted in single closing at low frequency and rhythmic chewing (3.5 to 4.0 per second) at high frequency, very much like the normal chewing speed of the conscious rabbit. Schärer and Pfyffer (1970) distinguished several different types of normal chewing movements in rabbits. Such patterns were also found in anesthetized animals by stimulating the posterior part of the anterior cortex, the amygdaloid nucleus, and the anterior hypothalamus. Each area produced one of the patterns of movement found in the conscious rabbit but which was different from that produced by other areas. Penfield found both opening and closing areas in human motor cortex (cited in Kawamura, 1964).

The plausibility of an amygdaloid input to the masticatory system is increased by Johnson's study of the fornix and hypothalamo-tegmental tract in the cat (1965). He found that fibers from the lateral amygdala proceed via the stria terminalis and longitudinal association bundles to the paraventricular and ventromedial nuclei of the hypothalamus. (Note the importance of the former for water balance - one of the nuclei in which ADH is made before later storage in the pars nervosa of the hypophysis; the latter is the traditional "satiety center" of physiological

psychology.) Fibers are traced from the ventromedial nucleus through the posterior hypothalamotegmental tract to the nucleus mesencephalicus profundus pars ventralis of the midbrain tegmentum. Morgane (1969) traced a similar path, leading to both ventral and central tegmental regions. Such a route would help to explain the fairly long latency observed for the amygdalar effects observed by Kawamura. The two paths both depend on connections through the reticular formation. In 1962 Valverde stated that at least one intercalated reticular cell, located partly in the reticular areas, was found between the cerebral cortex and the neurons of any cranial motor nucleus.

Chewing activity may be evoked by stimulating not only cortical areas and the others given above, but also putamen, globus pallidus, substantia nigra, lateral hypothalamus, anterior commissure, and reticular thalamus (Lund and Dellow, 1971). Some of these areas have been discussed. The first movement was usually jaw opening. Neither cerebral cortex nor cerebellum were necessary for chewing activity. Karamanlides (1968) found retrograde cell degeneration in Mes V only when the homolateral brachium conjunctivum was lesioned (and that occurred in just one animal), no matter how large the cerebellar lesion was. In rat, Cupedo (1965, 1970) found cerebellar connections of the Mes V root, though the number of connecting fibers was small. Most of them terminated in the vicinity of the primary fissure. Recently, Johnston (1970) tried to find evidence for direct sensory projections from the masticatory muscles to the cortex. By stimulating the masseteric nerve of the

cat electrically, he was able to record primary evoked responses in the contralateral first, second, and third facial areas of the sensorimotor cortex. But the stimulus strength necessary was greater than that assumed to activate group I fibers. Perhaps group II fibers provide the information. If so, their cell bodies must be elsewhere than Mes V, because chronic destruction of Mes V just rostral to Motor V did not change the evoked potential pattern recorded in the cortex in any discernible manner, compared to normal animals or compared to the unoperated side of the test animals. Johnston suggests that such projection may not exist for the jaw muscles, even if it is found in other (non-specified) systems.

Subsequent work utilizing cortical stimulation has concentrated on modification of the monosynaptic masseteric myotatic reflex. Sauerland *et al.* (1966) using cats, produced inhibition of the jaw jerk reflex (evoked by direct stimulation of Mes V) when the preoptic area of the cortex was stimulated at either the anterior sylvian gyrus or on the orbital surface. A variant, the so-called Hoffman reflex caused by stimulation of the proximal masseteric nerve and recorded from single units of the same nerve distally, has also been used to study the monosynaptic reflex (Nakamura *et al.*, 1967). This was inhibited by orbital cortex stimulation and the mechanism was found to be hyperpolarization of the masseteric mns, or postsynaptic inhibition. They believe that the suppression is exerted directly on the α mns which innervate masseter, without any intervention of the γ system

since the animal was immobilized with Flaxedil and the distal end of the masseteric nerve had been cut. Nor were cerebellum or ascending inhibition from the cord involved, since the cerebellum had been completely removed and the spinal cord was transected at C2. Further work has shown the existence of another form of cortically induced masseteric reflex suppression, this time by presynaptic inhibition (Sauerland and Mizuno, 1969). Two phases of suppression were found, the first at a conditioning interval of 10 msec, and the second at a conditioning interval of 40 msec (time between a single conditioning pulse to the coronal gyrus and test stimulation of Mes V to produce the masseteric reflex). The first type completely eliminated the reflex but lasted a very short time while the second was much less effective though it lasted considerably longer. The former was abolished by strychnine while the latter was eliminated by picrotoxin. The latter had the same time course as the cortically induced primary afferent depolarization of the mesencephalic tract neurons as measured in trigeminal and hypoglossal nuclei. (Remember that there are collaterals from Mes V to the hypoglossal nucleus!)

The trigeminal reflexes are modified by activity in other nerves. The linguo-mandibular reflex, jaw opening when the tongue is stimulated, is an example. Goldberg (1967) was able to show that lingual nerve stimulation caused EPSPs and spikes in hypoglossal mns while producing IPSPs in masseteric mns. Sumi (1970b) found that lingual nerve stimulation inhibited cortically evoked chewing and swallowing. This was considered to be a protective mechanism.

Nakamura *et al.* (1970) have shown that stimulation of the hypoglossal nerve can effect either inhibition or facilitation of the masseteric reflex via a polysynaptic route to Motor V. The masseteric reflex is also inhibited by a single shock to the vagus (Chase and Nakamura, 1968). Noxious paw pinching and rectal distension were both inhibitory to chewing movements (Lund and Dellow, 1971), showing interaction with noncranial nerves.

C. *EMG Studies*

The process of chewing has been studied through direct observation, cinephotography, cineradiography, and electromyography. Although animals have been used in a few of these, most of the work has been done on man.

Ardran and Kemp (1960) state that the rabbit has had much more practice in chewing than man, since it spends much of its waking life eating, and, as a result, is better at it. Using cineradiography, they compare chewing of "fresh green stuff" and "older dried material" by the rabbit with human chewing of barium impregnated oatmeal, a gelatin-barium "sweet" and licorice. From this, they conclude that the basic jaw movements are (as stated by Hildebrand, 1937):

1. An opening movement which was mainly straight down but which in certain humans swings over to the side opposite that on which chewing will take place.

2. A preparatory movement in which there is elevation and an outward swing of the mandible to the chewing side.
3. A crushing or grinding movement as the jaws are approximated and as the lower teeth move medially to the centric position.

They give a detailed description of biting, transport of the bolus to the cheek teeth, chewing, and tongue movements in the rabbit.

Hilemæe (1967) has made a similar study for the rat using both cinephotography and cineradiography, in combination with anatomical studies, to determine the probable functions of the masticatory muscles. Gold foil fillings in the mandibular incisors and first molars served as reference markers for tooth position in radiographic studies, as the rats ate radiopaque biscuit or bread and milk. Because my own study included EMG analysis of such movements, a fairly complete summary of her findings is relevant.

Hard food was actively incised, while the "mushy" bread and milk were sucked into the molar region of the mouth. The processes of incision and mastication (molarization) were functionally separate. She divided the movements of both incision and molarization into four strokes: "a preparatory stroke brings the teeth into a functional relationship; the second or incisive stroke is used in chewing; the third or power stroke reduces the food, and the fourth, recovery stroke, returns the mandible into position for the next cycle."

The difference in *incisive behaviour* observed when the rats were fed hard, medium or soft food was found to be due to variation in the time scale of the incisive stroke. The sequence commenced with the depression and protraction of the preparatory stroke to bring the lower

incisors below and slightly behind the upper incisors. The incisive stroke, elevating and protracting the mandible, carried the edges of the lower incisors into an edge-to-edge relationship with the upper incisors, thus separating a particle of food or bite. If the food was hard or fibrous, a single incisive stroke failed to separate a bite and was not completed; instead, the stroke was rapidly repeated several times in a chopping or chiseling motion until a bite was removed from the body of the food and the stroke was carried to completion. For soft food, the cycle was interrupted during the incisive stroke, the mouth being open and the material sucked into the oral cavity, the stroke was completed when a suitable volume of food had been ingested. The recovery stroke of incision carries the mandible upward and backward so that the edges of the lower incisors are moved across the lingual bevel of the upper incisors.

Mastication began after the ingestion of four or so bites or a suitable volume of bread and milk. This process consists of up to thirty complete masticatory cycles during which three boluses were swallowed. The preparatory stroke of mastication involves the elevation and retraction of the mandible from a depressed position, to bring the lower first molar below and behind the upper one; the power stroke is a combined protrusive and medial movement of the mandible carrying the lower molars anteriorly and medially across the upper molars; the mandible is then moved downward and backward in the final recovery stroke.

Transition between the anterior position of the mandible used in ingestion and the posterior position in chewing is effected by translation of the mandible through the rest position. This is a consistent, reproducible position of the mandible and is adopted when the rat is at rest and between bouts of feeding or other oral activity. The lower incisors are positioned behind the upper incisors, and the lower first molar is held slightly anterior to the upper molar and is separated from it by the inter-occlusal or freeway space.

She concludes, on the basis of anatomical studies combined with estimations of the probable force capabilities of the muscles, that anterior temporalis acts with deep masseter and the pterygoids to stabilize the mandible and also to elevate the jaw. Mandibular

retraction is effected by posterior temporal, antagonized by digastric when retraction and depression occur together (as in the preparatory stroke of mastication). Deep masseter acts with superficial masseter in the power stroke of molarization while the infra-orbital and anterior deep masseter perform this function in incision. The major phasic muscles, posterior temporal and superficial masseter, are mutual antagonists: the former effects mandibular retraction while the latter is responsible for gross protraction (as in the transition from molarization to incision). Either may be antagonists of digastric when retraction or protraction is associated with jaw depression. Superficial masseter can produce movement to the contralateral side. Internal pterygoid effects lateral movement as well as controlling the position of the mandibular condyle. It may or may not act as the "trigger" in mandibular depression. Digastric is the major jaw depressor.

O'Dell, Todd and Bernard (1970) report that "an unsuccessful attempt has been made to record electromyographically the rat's masticatory activity, but as far as we know, no one has succeeded with either rat or rabbit". They studied muscle activation in passive lateral jaw movements of rat and rabbit, finding that such movement is actively opposed by the ipsilateral medial pterygoid in the rabbit, and by ipsilateral medial pterygoid and contralateral masseter in the rat.

In the chronic decerebrate rat, Woods (1964) observed the basic components of eating behaviour; that is, rats would hold

an object or piece of food in their paws, bite it, try to chew it and swallow the pieces. The activity was largely ineffective. Most of the food fell out of their mouths. Either food or inedible objects would be treated in the same manner. These animals could perform functional grooming, however, and succeeded in keeping themselves clean. In each case, the brainstem had been transected "at an upper mesencephalic level". Thomas (1969) has obtained incisive chewing in the acute decerebrate rat.

Many EMG studies have been made during active chewing in man and will not be discussed here (for reviews, see Carlsöö, 1952; Kawamura, 1964; Møller, 1966). The most complete studies of active chewing in man to date are the monograph of Møller (1966) and the series of papers by Ahlgren (1966, 1967, 1969; Ahlgren and Öwall, 1970). Møller gives a full discussion and evaluation of EMG methods and then uses them to study chewing and swallowing in thirty-six subjects. This is followed by an attempt to relate EMG activity to the anatomy of the muscles. Møller's subjects chewed white bread and apple, to give a measure of reduction in size and consistency of the bolus, and gum, for activity in which bolus size and consistency remained constant. EMG records were taken on a two-channel recorder using right anterior temporalis as reference and comparing its activity to that of posterior temporalis, masseter, medial pterygoid, lateral pterygoid, digastric, mylohyoid, and lips in turn. Activity was taken at rest, during the "bite" (incision), and for the first five to six chewing strokes. In addition, make and break of tooth contact was established by electrical contact

of stainless steel bands mounted on an upper and lower incisor; these made contact only in the intercuspal position, though electrical contact was also recorded from posterior teeth when existing fillings made this practical. Onset and cessation of activity was determined from the direct EMG recordings, while the mean voltage tracings obtained through an RLC filter were used for the amplitude parameters. Each chewing stroke was characterized by twelve time and amplitude parameters, with an additional three to six parameters being measured for "secondary activity" (that is, "activity appearing constantly in each chewing cycle in addition to the primary action which is the activity in the elevators during closing and in the depressor and lip muscles during opening"). He found that the duration of the chewing cycle was longer for bread than for apple and was longest for gum. These differences were due to differences in the opening movement. During natural chewing (bread and apple), the greatest degree of activity was found in bread; during unilateral gum chewing, largest maximal mean voltage was found on the ipsilateral side. Usually right anterior temporal (his reference muscle) and left anterior temporal muscles were innervated symmetrically for natural chewing but activity occurred first on the ipsilateral side for gum. Masseter was activated at the same time as anterior temporalis and had its greatest amount of activity for chewing bread. Contralateral masseter was activated first in gum chewing, but the two sides worked together in natural chewing. Internal pterygoid was the first of the elevators to be activated. Of the jaw depressors

external pterygoid had the strongest activity in opening (primary activity) but was also active with the elevators (secondary activity). Primary activity was the same for apple and bread but secondary was 30% stronger for bread. Digastric (a depressor) was always activated at the same time as the maximal activity of anterior temporalis (an elevator). Mylohyoid reached its maximum activity before digastric did so, occurring while strong activity was present in right anterior temporalis. Tooth contact was made shortly after the maximal activity of the reference muscle and lasted 70 msec longer than activity in that muscle. This is accounted for by the delay between electrical and mechanical activity of the muscle (about 100 msec for natural chewing, according to Møller). Chewing contact occurred later on incision than on molarization, both for make and break. The variation in the time course and degree of activity in the reference muscle during two sequences in the same test session (in terms of standard deviation of the difference) was four to seven times larger than variation from errors of measurement. The variation increased by from 30 to 50 percent when comparison was made between experiments on different days; this is attributed to change in electrode position.

Ahlgren's original study (1966) was performed on eighty children and compared chewing patterns and muscle activity (obtained from cinephotography and electromyography, respectively) between children with normal occlusions and those having various types of malocclusion. The equivalent of my bipolar EMG electrodes

(see Appendix) were placed at standard positions on right and left masseter and right and left temporalis. Simultaneous "average integration" (showing the average value of the area per unit time) or full wave area integration (an integrated curve showing continuous growth of the area derived from the EMG potentials, used as a direct measure of total electrical activity) were obtained from specially built on-line integrator units. In addition, a gnathodynamometer was used, both to check linearity between muscle tension and integrated EMG and to "get a meaningful value out of the integrated electrical activity". Analyses on the EMG data were as follows: 1) Thirty movements for each subject (ten from gum chewing and twenty from peanut chewing) were analyzed on direct EMG and average integration for coordination and duration of activity in masseter and temporalis. 2) Using the average integration of the EMG, thirty chewing movements of each subject were analyzed for maximal amplitude of the EMG pattern. 3) The total electrical activity from each muscle (the full wave area integration) was determined for 10 sec of gum chewing. They found a "silent" period in all records which corresponded to tooth contact. In peanut chewing, temporalis activity appeared first. These points were further discussed in later papers. Sixteen different chewing patterns were found for gum chewing (that is, patterns of muscular activation), where load and speed of movement had been controlled, while twelve patterns were found for peanut chewing. For gum, the most frequent pattern (44%) began with contraction of ipsilateral temporalis, the three other muscles contracting later

and all together. Peak activity and duration of activity was simultaneous in 80% of the cases. For chewing peanuts, the most characteristic pattern (50%) was simultaneous onset of activity in both temporal and both masseter muscles, with peak of contraction occurring simultaneously most of the time (82%). EMG activity started at a low level and increased to the end of the closing phase. The cycle time for gum chewing was 16% longer than the cycle for peanut chewing. For gum chewing, temporalis was active longer than was masseter, and EMG activity comprised 38% of the total cycle time.

In the second Ahlgren study (1967), mandibular movement and EMG activity were analyzed together for ten children chewing gum, peanuts and carrots. The cycle is divided into opening, closing and occlusal phases - the latter being the time the teeth are in the intercuspal position. "The occlusal phase also corresponds to the interval between the 'occlusal silent period' in the EMG and the termination of the EMG pattern of the masticatory cycle " (Ahlgren and Öwall, 1970). "Integrated" EMG in this study is the average integration of the previous study. Again, temporalis and masseter were used. No activity was recorded during active jaw lowering. Activity in both appeared approximately at the start of closing, though actual time of onset was related to the rate of the movement. (In a very fast movement, EMG activity might appear exactly at or even before jaw closure began.) EMG activity increased to the end of the movement, but a short "silent" period appeared in the EMG at the start of the occlusal phase.

Maximal integrated EMG came before this silent period. About 75% of the EMG was recorded during the closing phase, that is, before the silent period occurred to signal onset of the occlusal phase. The silent period is believed to be a protective mechanism, that is, to bring about jaw opening.

In the final studies of this series (Ahlgren, 1969; Ahlgren and Öwall, 1970), the silent period in the EMG records of the jaw elevators is related to tooth contact, and muscle activity is related to chewing force. A silent period was found in most EMG records during both chewing and biting (1,000 records were examined). In the early cycles during the chopping strokes of peanut chewing, more than one silent period was found. This silent period coincides with tooth contact. Peak activity as determined from the integrated EMG record could occur either before or after this silent period. Maximal chewing force is developed during the occlusal phase of mastication and outlasts the occlusal phase. Peak EMG activity precedes maximal chewing force by 41 msec in humans. The integrated EMG can be used as a reliable index of chewing forces when a homogeneous bolus is being chewed (chewing gum) but not otherwise. A study by Atkinson and Shepherd (1967) reached the same conclusions about time of maximal chewing force. Their work showed that "significant forces were not developed until the teeth were almost in contact and that after contact, the force increased without further movement being detected".

D. *Control Theories*

The two major theories of mastication at present are the chain of reflexes theory, almost entirely peripheral in control, and the alpha-gamma linked central oscillator.

Sherrington's reflex chain, initiated somehow from the cortex, and Rioch's variant, with cortically initiated jaw opening and jaw closing centers, have been described above. Kawamura's work might be considered to support the possibility of such centers. The theory has been stated explicitly by Jerge (1964): "The fundamental mechanism underlying cyclic jaw motion appears to be the interaction of jaw closing muscle proprioceptors and intra-oral pressure receptors of the teeth and soft tissue ... The jaw musculature appears to have a stretch reflex mechanism only in the jaw elevator or closing muscle group which provides a mechanism for reversing the opening movement ... Reflex opening is accomplished by the aggregate influence of receptors for touch and pressure in and adjacent to the mouth ... Thus, a cyclic interaction of the jaw closing muscle myotatic reflex and the jaw opening reflex keeps the mandible in motion as long as there is food between the teeth." More recently, the work of Kidikoro *et al.* (1968) on the reflex organization of cat masticatory muscles and of Chase and McGinty (1970) on cortical initiation of cyclic jaw movements have been cited as support for the reflex control theory.

The central oscillator concept reviewed by Pearson (1972) is beginning to receive support, though certainly most of the

evidence is not yet in. It was originally proposed by Magoun, Ranson and Fisher in 1933. Such an oscillator would supply a basic pattern of alternating facilitation and inhibition through simultaneous activity of α and γ mns to elevators and depressors in the masticatory system. Feedback reflecting peripheral conditions then modifies the basic ongoing pattern to take care of load variation, noxious inputs, and the many other variables found in normal chewing. Such an oscillator was included in Dellow's hierarchy of reticular system (the probable location of the oscillator - see above), stem reflex system, and supra-segmental system.

What *is* the evidence to date for alpha-gamma coactivation and/or a central oscillator in the masticatory system? Davey and Taylor (1966) say that to prove a movement is supported by γ activation requires showing that the spindle afferents either increase their rate of firing during active shortening or else "slow less than during the same amount of passive shortening". They were able to show such units in Mes V when "active movements" were obtained in lightly anesthetized cats by putting fluid into the mouth to cause a reflex swallow and mouth closure (Taylor and Davey, 1968). They were unable to show that the afferent discharge preceded jaw closure, which they wanted to do as they were trying to find evidence for Merton's theory. Nevertheless, this work is important since it is the first to indicate any γ activity in mastication. Sumi (1970a) has shown that the rhythmic pattern in hypoglossal mns during cortically evoked chewing does not change

when motoparalysis is produced with gallamine triethiodide, even though jaw opening and jaw closing movements no longer occur. Using anesthetized rabbits, Dellow and Lund (1971; Lund and Dellow, 1969) found continuing rhythmical discharges in trigeminal and glosso-pharyngeal nerves after intrafusal fibers had been blocked with gallamine (Flaxedil). Although not mutually inhibitory when stimulated antidromically, switching occurred between antagonist mylohyoid and masseteric mns. The discharge rate between 25 to 80 Hz was independent of the rate of stimulation. Summation and inhibition occurred during motoparalysis with Flaxedil. Removal of all inputs from mouth, peripheral respiratory receptors, and vascular mechanoreceptors did not change the rhythm, as recorded in the hypoglossal nucleus. Random stimulation of the internal capsule did not change the rhythmical recordings from the hypoglossal nerve during motoparalysis.

Murphy (1967) has advanced the hypothesis that periodontal or dental damage during chewing is prevented by alpha-gamma coactivation. The nervous system forecasts the force necessary to crush the bolus. The γ route is said to set the shortening of the spindles and the α route causes these muscles to contract until they are in alignment with the preset spindles. Then afferent impulses from the spindles would stop and so would contraction of the muscle. No evidence was given to support the hypothesis.

III. STATEMENT OF THE PROBLEM

The reflex theory of mastication, first proposed by Sherrington in 1917, is widely held today. It has received recent support from Jerge (1964), Kidikoro *et al.* (1968) and Chase and McGinty (1970). Contrary evidence has been found by Taylor and Davey (1968) and Dellow and Lund (1971), as discussed in detail above. In all of these studies, subject animals were to some degree non-normal: they were under anesthesia, were paralyzed, were decerebrate, or were receiving electrical stimulation from implanted brain electrodes.

It was felt that exclusive use of non-normal animals limited the generality of these findings. Therefore it was decided to test the reflex theory further by recording from a freely-moving, non-anesthetized, non-stimulated animal as it ate normal food.

To establish these normal chewing patterns, records were made of afferent input to the system, represented by the mesencephalic nucleus of the trigeminal nerve, and of efferent output, represented by three masticatory muscles. The electrical activity of Mes V was recorded by a multiunit mono- or bipolar electrode stereotactically placed in the nucleus, while the electromyographic records of masseter, temporalis, and digastric muscles were made with chronically implanted bipolar silver wire EMG electrodes. Jaw position was recorded through an inductance transducer with its parts mounted on the animal's lower jaw and in the head connector assembly. Several foods were used in this study.

IV. METHODS

The subjects of this study were Wistar white rats, weighing from 200 to 300 g. 200 g rats were always used for brain implant studies; somewhat larger ones were used for the EMG and jaw position transducer assemblies, because of the larger amount of skull surface needed to mount them. Both male and female rats were used, though females were generally more cooperative. The animals were housed in the Animal Services facility of the Dentistry-Pharmacy Center. They were maintained in individual hanging cages fitted with outside food racks, since the head assembly tended to get caught in the food rack of plastic shoebox-type cages. Animals were fed the standard pellets of Rockland Mouse/Rat Diet, *ad lib.* (Rockland Lab Animal Diets, Toronto, Ontario).

A. The Head Assembly

i) The basic pedestal.

Figure 3 shows Rat 19 fitted with the head assembly used in these studies. When the picture was taken, the animal had been wearing the assembly for four months, with no apparent ill effects. This particular arrangement consists of three pairs of bipolar EMG electrodes in temporalis, masseter, and digastric muscles. Animals have been maintained for similar time periods with electrodes implanted in the Mes V, often with one or more sets of bipolar EMG electrodes as well; these animals also had no apparent problems with their electrode assemblies.

A



B

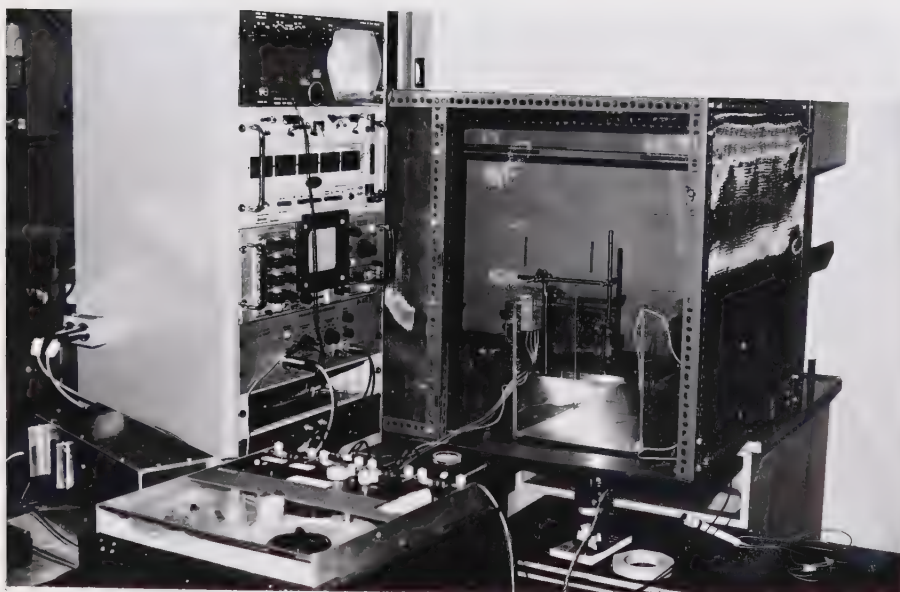


Figure 3. A. Rat 19 eats pudding. Head assembly includes three pairs of bipolar EMG electrodes, in temporalis, masseter, and digastric.

B. Basic recording arrangement.

The assembly itself is illustrated in Figure 4. This example consists of a monopolar brain electrode, one pair of EMG electrodes, and a ground wire; however, many combinations of electrodes and many sizes of mounting pedestal were used. They have ranged from a single brain electrode and a ground to the seven-connection assembly used for either three pairs of EMG electrodes or the bipolar electrode-jaw movement transducer assembly (Fig. 5). Chief limitations seem to be the size of the animal's skull, number of preamplifiers available, and surgical talent, rather than any problem of animal discomfort. The rats are capable of wearing an amazing number of leads when implanted by the techniques discussed below.

To make the basic pedestal, the wide Amphenol strip connector (0.001 in. center) is cut to size and, if necessary, two or more are glued together with quick setting epoxy resin. Using the grinding wheel of a bench dental drill, a groove is made on all sides of the assembly, just above the base. Similarly, exit channels for ground and EMG wires are cut. Gold-plated Amphenol inserts, soldered to the type of electrode required, are then carefully positioned flush with the base of the assembly, and, where necessary, covered with fine polyethylene tubing as insulation. The entire base is coated with a thin layer of epoxy to secure the insulating tubing and to prevent any possible movement of the inserts when the animal is connected to the recording leads. After hardening of the epoxy, the brain electrodes are insulated and allowed to dry overnight.

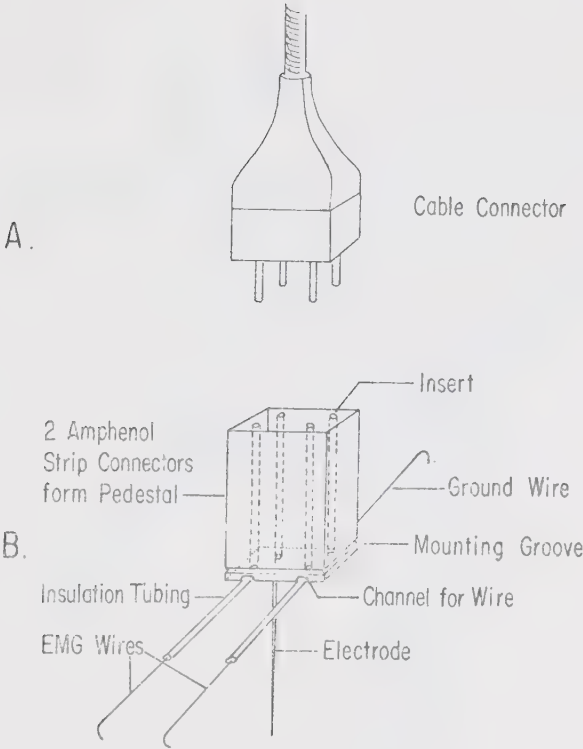


Figure 4. The head assembly.

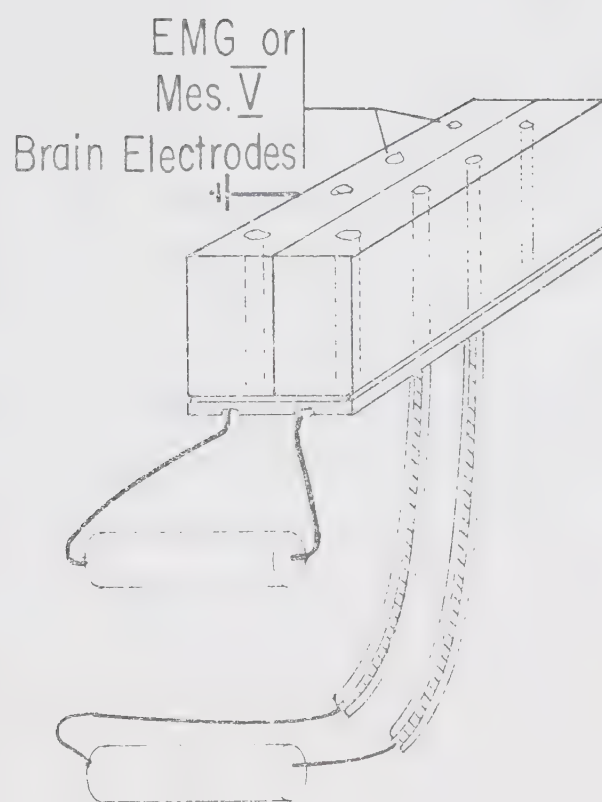


Figure 5. Jaw movement transducer assembly.

ii) *Electrodes.*

Mes V electrodes were usually stainless steel insect pins (size 00) insulated with a polyurethane coating ('Endura EX-2C Clear 100', Endura Mfg. Co., Ltd., Edmonton, Alberta; equal parts of Compound A, Compound B, and acetone were mixed). Tip exposure was caused by slight retraction of the insulation as it dried overnight. Microscopic examination showed an exposed tip of 10 to 15 μ . Electrical resistance ranged from 50K to 150K ohms when tested by the method of Sidowski (1966); that is, by placing the electrode connected to one side of a battery ohm-meter in saline and connecting the other side of the meter to the saline directly. Insulation was checked by visual examination under a microscope and/or by running a saline-soaked wick connected to the ohm-meter up and down the wire. When bipolar electrodes were used, they were made in the same way from insect pins and mounted in pairs in the head assembly, such that the interelectrode distance was about 2.7 mm. The posterior electrode was somewhat longer than the anterior, so that the posterior one would be positioned in Mes V while the anterior lodged in an indifferent area of the animal's brain with respect to chewing, usually a part of the cortex. Thus, differential recording methods could be used to produce a much better trace. Sometimes commercial microelectrodes were used (Transidyne 414-20 and 404-10). These were of platinum-coated stainless steel or tungsten, 1 μ tip diameter, 2 μ exposed tip length, insulated with Epoxylite. The resistance of the stainless steel electrodes was 10 M Ω while the tungsten was rated at 9 M Ω .

EMG electrodes were made of light silver wire (0.005 in.). Polyethylene tubing (Intramedic PE 10, I.D. 0.011 in., O.D. 0.024 in.), cut to size and slid over the wires served as insulation and gave mechanical protection to the fine wire. A heavier silver wire (0.008 in.) was used for the ground connection. Although the ground wire was sometimes insulated with the polyethylene tubing, the acrylic used to anchor the entire assembly to the skull was normally sufficient.

iii) *Jaw-movement transducer.*

This arrangement is shown in Figure 5. The assembly was made as described above but with the addition of two small cylindrical coils having an inductance of 1,000 μ h encased in a phenolic mold (J.W. Miller, 9230-92, 0.250 in. long, 0.095 in. dia.). For the coil on top of the animal's head, the connecting wire was simply bent as illustrated and soldered to the pedestal insert, so that the coil was placed as far forward as possible. The wires of the lower coil were bent as shown to provide an attachment at each end for sutures. Silver wire (0.008 in. dia.) insulated in the usual manner with polyethylene tubing, was used for the connection across the rat's cheek. Since the coils were contained in a phenolic mold, it was necessary to cover the lower coil with the polyurethane coating. The upper coil would be completely surrounded by dental acrylic when fixed to the animal, so an additional biological inert covering was not necessary.

B. *Surgical Procedure*

All animals were given a preanesthetic dose of atropine sulfate (14 $\mu\text{g}/\text{Kg}$, i.p.). The head and cheek were shaved and the animal was placed in the stereotaxic apparatus. When possible, the animal was positioned without damaging the tympanic membranes, since animals as normal as possible were desired for the experiments.¹ A midline incision was made, exposing the top of the cranium. The skin was reflected and the bone carefully scraped clear. After cleaning with a damp gauze sponge, the bone was dried thoroughly with compressed air. Bleeding from either bone or surrounding tissue was stopped by application of a silver nitrate stick.

The head assembly was fixed to the microdrive of the stereotaxic apparatus and the head position was adjusted. The exact coordinates for the implant were determined and the spot marked with a lead pencil mark. At the same time, positions for the skull screws were determined. The electrode assembly was swung out of the way and from three to four steel watchmaker's

¹ For this reason, the stereotaxic method of Hart (1969) was used, in which the horizontal plane is determined by setting the suture intersections bregma and lambda at the same level. Bregma is then used as the base point to determine all other coordinates. This method was used in conjunction with König and Klippel's stereotaxic atlas (1963) and also with an atlas prepared photographically by the author, using the same strain of rats as the experiments. Adaptation to the axes of König and Klippel was quite rapid if bregma was taken to be 7,190 μ , an assumption borne out by the work on the animals used. The horizontal plane was the same except for raising it 6 mm, to lie along the top of the skull instead of 4.9 mm above the plane passing through the interaural line.

screws were placed in the bone.² Then the hole for the electrode was made with a small bur in a dental air rotor. This was a fairly sensitive procedure, since the mesencephalic nucleus passes beneath the transverse sinus.

During positioning of the brain electrode, guidance was often obtained by connecting the animal to one preamplifier and the recording instruments, including a loudspeaker; the final electrode depth was then determined by reaching the appropriate "crackling", "brush-fire" or roaring sounds of Mes V (Corbin and Harrison, 1940; Smith, 1969). The ground wire was wound around one of the skull screws and the excess wire clipped (in some experiments this wire was led under the skin at the front of the incision). Any EMG wires were held in position by weighting them with a small clip. Self-curing acrylic resin (Caulk Orthodontic Resin, L.D. Caulk Co., Toronto, Ontario) was placed over and around all screws, wires and the head assembly itself, to cover the entire top of the head. When the acrylic was dry, the animal was removed from the stereotaxic apparatus for placement of the EMG electrodes.

An incision was made perpendicular to the original one and midway between eye and ear, extending down the cheek. If electrodes were to be placed in the digastric muscle, this incision extended from the top of the head, down the cheek, and beneath the mandible. Electrodes were located approximately in the middle

² Since the screws did not normally touch the underlying dura, it was not necessary to use stainless steel screws. However, when the screws did touch the tissue below, an area of necrosis resulted.

of the muscle (Fig. 6) such that a line connecting the exposed wire of a set would be perpendicular to the direction of muscle fibers and thus in or near the "innervation band" or zone containing the motor end plates of the muscle, determined by Karlson (1965) to be equidistant "from both ends of the muscle and almost perpendicular to the fiber direction" for the masticatory muscles of the rat. The electrodes of a set were placed 1 to 2 mm apart. To set the electrodes, excess insulation was cut with a single-edged razor blade and slipped off; the wire was threaded into an ophthalmic suture needle and a small stitch taken into the muscle; the silver wire was carefully drawn through the tissue, bent back on itself and secured by a turn around the standing part of the wire. The excess was clipped off, leaving about 1 mm in the muscle. Care was taken to allow plenty of slack in the wire to prevent displacement of the electrode as the animal chewed. This was accomplished by laying the wire in a wide curve, as shown in Figure 7, and maintained simply by closing the skin again and securing it with closely spaced interrupted sutures. Finally, the incision at the top of the head was closed around the pedestal. When the wires were checked after the animal had been sacrificed, they were held in position securely by an investing layer of fascia.

A similar procedure was followed to place the coil assembly. It was located as far forward as possible so that the upper coil would be nearly in line with the lower to maximize their separation as the jaw opened. The lower coil was slipped into a "pocket" formed by the skin under the mandible, as far forward

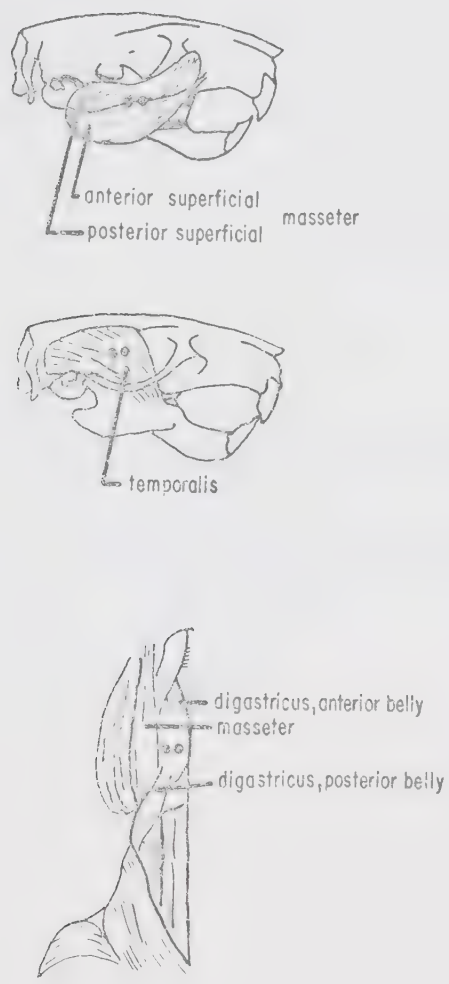


Figure 6. Placement of EMG electrode pairs (from Greene, 1955).

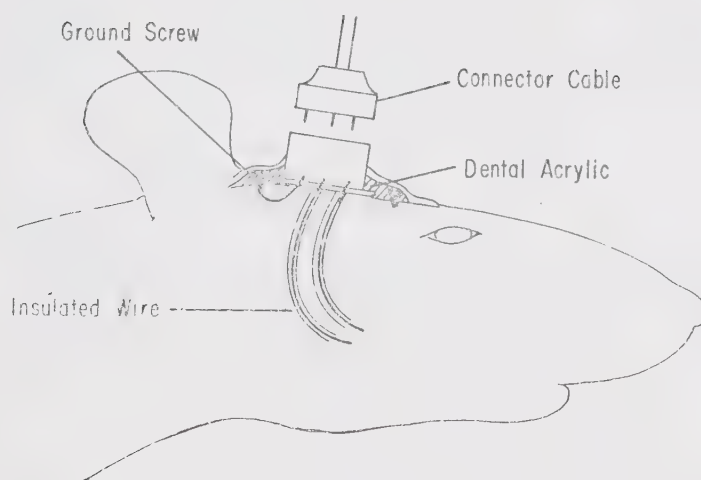


Figure 7. Permanent implant of EMG electrodes.

as possible and below the roots of the lower incisors. It was secured to the underlying fascia by sutures at both ends of the coil. Since the wires between the lower coil and the pedestal were sometimes too long, excess wire was bent into an "S" shaped curve and the skin closed over it in the usual manner. These assemblies were less easily tolerated by the animal than either brain or EMG electrodes. In one instance, the animal rubbed a hole in his skin at the far end of the lower coil, that is, at the uncut end of the "pocket" containing it. Records had to be made as soon as possible after surgery, due to the likelihood of having the lower coil displaced or a connection broken as the rat hit his extended "chin" while eating or in other normal activity.

Since some of the operations were quite long, either ether anesthesia or, if only suturing remained, an infiltration of lidocaine (Xylocaine HCl 2%, with epinephrine 1:100,000, Astra-Hewlett, Mississauga, Ontario) was used to extend working time. After completion of surgery, each animal was given 50,000 units of penicillin G, i.m., before being returned to his individual cage.

To prepare the decerebrate animals, a hot scalpel blade is introduced into the brain just anterior to the superior colliculus. The entire brainstem is severed. The anterior brain is left *in situ*, since its removal by suction causes damage to blood vessels and swelling of the brainstem. (Under such conditions, accurate localization of subcortical structures becomes almost impossible.) The plane of the incision is anterior to the red

nucleus and posterior to the interpeduncular nucleus. Thus, the connection to thalamus is severed while the midbrain remains intact. The operation was carried out under methoxyfluorane (Penthrane, Abbott) anesthesia.

C. *Recording*

The basic recording arrangement is illustrated in Figure 3B, while Figure 8 is a block diagram of the arrangement for recording either from Mes V and two muscles or from three different muscles. The connector cable from the head assembly of the animal was supported overhead by a carrier which allowed the subject to move freely around the observation cage. The animal was grounded through the head assembly as previously described and also by contact with an aluminum plate which formed the floor of the cage. The head connector cable led to a junction box on the side of the cage, and from there shielded cables proceeded to three Tektronix 122 differential preamplifiers (frequency response was 250 to 2,500 Hz for brain recording, 8 to 1,000 Hz for EMG recording). Output from the three preamplifiers was monitored on a Tektronix R564B storage oscilloscope (CRT) fitted with a four-trace amplifier (3A74; time base, 2B67). The additional trace was used to monitor the output of the tape recorder. All signals were simultaneously recorded on a Thermionics T3002 four speed, four-channel FM tape recorder. Tape gains were usually set to be exactly the same as the preamplifier output. Voice comments or the sounds of incision while an animal chewed a large

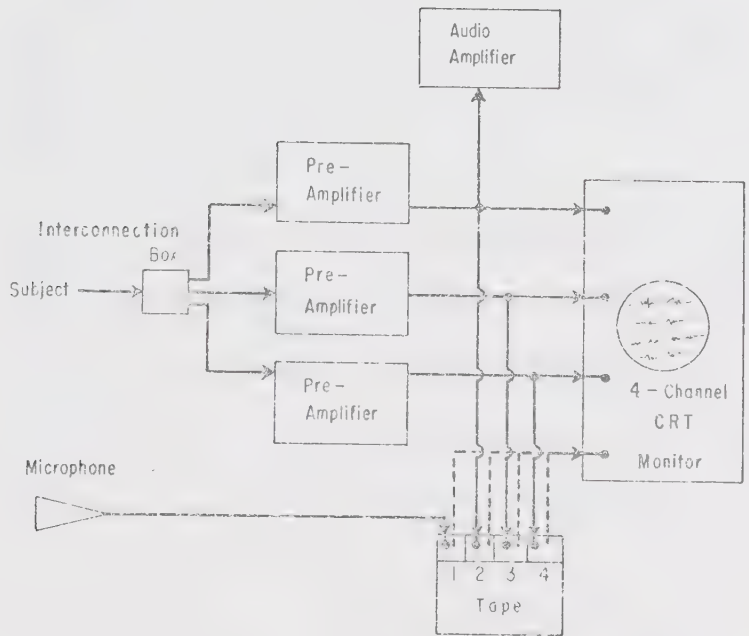


Figure 8. Block diagram of basic recording arrangement.

food pellet were recorded on the additional channel. Also, this track or any one of the preamplifier outputs could be monitored through the audio amplifier.

This arrangement was altered for special purposes. For work on anesthetized animals, the input to the microphone could be used to trigger the oscilloscope, or it could be triggered by the five-figure Devices Digitimer, a digital time interval marker and event release. This was often used in conjunction with the Devices Mk. IV isolated stimulator.

Another variation, shown in Figure 9, was used to record from the jaw movement transducer assembly. As before, EMG or brain electrode signals go via the differential preamplifier to the tape and are monitored on the four-trace amplifier of the CRT. A 20K Hz signal from a Tektronix carrier amplifier (3C66) was applied to the head coil. The lower jaw coil acted as a receiving aerial, the magnitude of the signal depending upon the distance from the head, or transmitting, coil. The received signal was applied to the same carrier amplifier where it was decoded to give an indication of jaw movement (Hannam, Matthews and Yemm, 1968). The transducer is non-linear and was used only to show relative time of jaw opening and jaw closing in reference to either masseter EMG or Mes V activity.

Recording from the decerebrate animals was done with a Mentor N-740 extracellular preamplifier, frequency response 100 to 2,000 Hz. EMGs were recorded with concentric needle electrodes made from an outer 20-gauge modified hypodermic needle around a #00 insulated insect pin. These preamplifiers were Tektronix Type 3A9

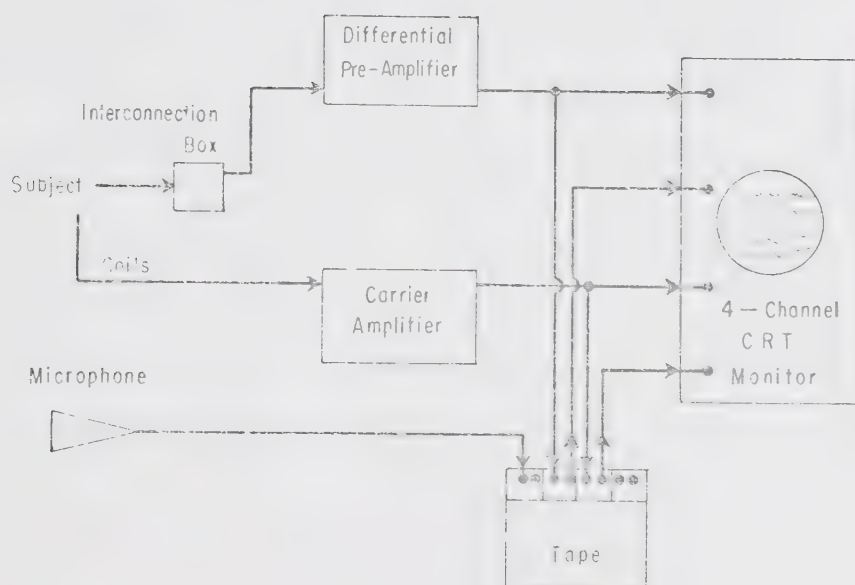


Figure 9. Block diagram of basic recording arrangement used with jaw movement transducer.

differential amplifiers set for a frequency response of 8 to 1,000 Hz. The ground was connected to muscles at the back of the neck.

Stretching and/or vibration of the jaw elevator muscles during some experiments was accomplished by attachment of the mandible to a vibrator (LTV 201 Shaker, ± 2.5 mm stroke) controlled by length feedback from a displacement transducer (Hewlett Packard 24DC DT-100). To produce stretch or vibration, the desired waveform from a function generator (Hewlett Packard 3310A) was resistively fed into the control amplifier (modified from the Super Tiger monaural amplifier with power supply, Southwest Technical Products, San Antonio, Texas). The output from the length transducer was recorded on one tape channel and/or monitored on the CRT. 0.2 mm vertical movement was represented by 1 v uniformly throughout the range of the transducer. The trace was reduced to one-half of its base value at 160 Hz for a setting of 0.2 mm, 150 Hz for 0.4 mm, and 140 Hz at 0.6 mm. Although several different types of attachment to the mandible were attempted, the only practical method was connection to the puller by a loop over the lower incisors. Because the two halves of the rat mandible are not fused at the symphysis, and because of the very small amount of bone in the base of the lower jaw (most of which is merely a thin layer around the incisors), rigid attachment to the vibrator through a bone screw or a piece glued with epoxy was not practicable. The connecting loop over the lower incisor was made from a piece of wire separated from the metal of the puller by a short length of acrylic rod. This non-conducting segment was necessary due to the great amount of electrical inter-

ference otherwise obtained in the record. In addition, the vibrator was positioned beneath the shielded cage, as shown in Figure 3B. A small hole in the floor admitted the link to the animal, but most of the electrical interference was eliminated. One difficulty with this link, of course, was the possible attenuation of the vibration or pull before it was transmitted to the jaw muscles.

D. *Histology*

After finishing experimental work, the animal was given pentobarbital anesthesia and sacrificed by perfusion with isotonic saline followed by 10% formalin. Histology was done by the photographic method of Hutchinson and Renfrew (1967). Frozen sections were cut at 50 μ and placed on a slide. These were photographed with light coming obliquely through the section from below. The structures of the brain, both fiber tracts and outlines of nuclei, appear clearly, with a minimum of distortion. It was often possible to get a complete electrode track in one section. Photographs were taken on Pan X film with a Miranda Sensorex single lens reflex camera (1:1.8 lens, focal length 50 mm). The camera was fitted with a $\times 5$ ocular and a bellows, so that finished negatives are twice actual size. Since Pan X is a very fine-grained film, enlargement to almost any desired size could be made with excellent preservation of detail.

The sections for the atlas were prepared in the same manner, taking 50 μ sections through the entire brain of two 200 g

rats. In addition, a series of 10 μ sections were prepared from the caudal half of the rat brain, using three different stains on paraffin-embedded sections. These were haematoxylin and eosin, solochrome cyanin, and Luxol fast blue. This series served as a more accurate guide to the location of mesencephalic nucleus and tract in the animals used, since cells, myelin and a combination of both were stained.

E. *Data Analysis*

Considerable information was obtained by examining the taped record on the CRT, either directly or after modification by the integrating system described below. Photographs were taken directly from the CRT screen using a Tektronix oscilloscope camera and Polaroid Type 107 film. At times, where experimental data was not being tape recorded, it was necessary to photograph traces after storing on the screen. Some detail is lost by this method.

Although such short sequences are useful, they show only a small part of the ongoing chewing process. To obtain a permanent record of normal chewing patterns, the method illustrated in Figure 9 was devised. Figure 10B gives a sequence of signals as they pass simultaneously through the components of the integration system used in this study. The top trace is a single burst of activity as recorded from Mes V. In the center trace this has been full-wave rectified, and in the bottom trace the rectified signal has been passed through a Paynter filter, that is, through a third order low-pass filter with an averaging interval of 10 msec (Gottlieb and

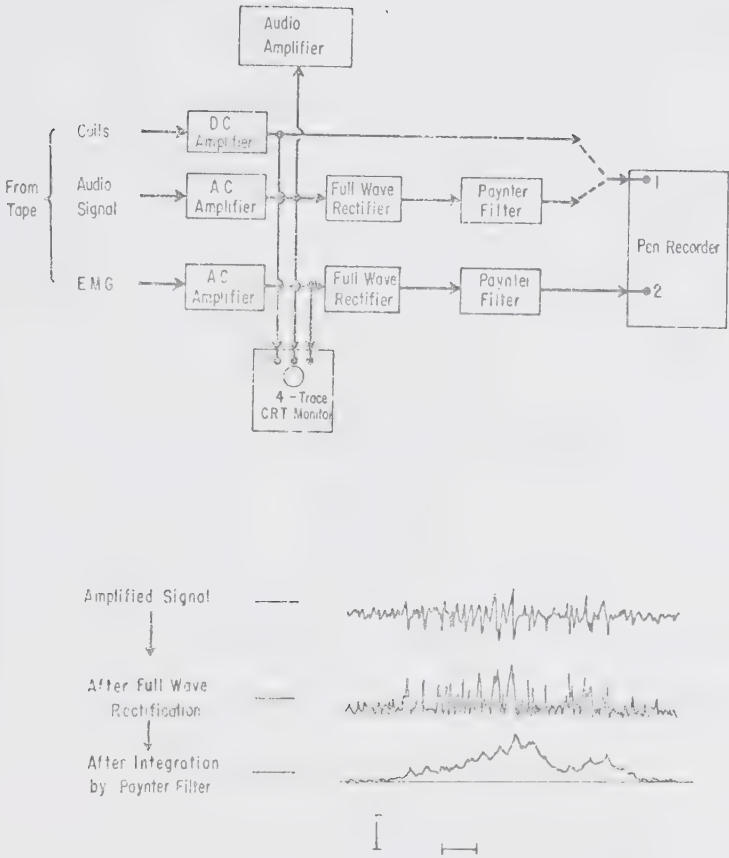


Figure 10. Data Analysis. A. Flow diagram. B. Signal Modulation.

Agarwal, 1970). The filter reduces the signal bandwidth but preserves the leading and trailing edges of the burst of spikes.

Figure 10A is a block diagram of the arrangement used to convert the taped signals to a written record. The AC and DC amplifiers, full-wave rectifiers, and Paynter filters in the diagram are all signal modulating units plugged into an operational amplifier manifold. Two treatments of the taped information are shown. 1) The EMG (or brain signal) and the audio signal each pass through an AC amplifier, full-wave rectifier, and Paynter filter before entering the DC amplifiers of a Hewlett Packard pen recorder (amplifiers, HP 8801A; pen recorder, HP 7702B). 2) The signal from the jaw movement transducer passes directly from the DC amplifier of the operational amplifier manifold to the DC amplifier of the pen recorder. All amplified signals were monitored on the CRT, both to determine the tape sections to be used and to adjust the amplitudes of the traces.

All measurements discussed below were obtained from the average integration records which resulted from this process. Means, standard deviations, and confidence intervals (at the 95% level) were determined using standard methods (Downie and Heath, 1965). Usually they are based on twenty-five consecutive cycles. All statistical comparisons concern molarization, since it is the most uniform stage of chewing. "Cycle period" is the time from onset of activity in masseter to onset of masseter activity in the next cycle.

The numerical values in this study are presented as aids

to description of the patterns encountered. They are not quantitative studies in the rigorous sense, for several reasons. Due to the fairly small size of the population studied, and also the very small size of the subjects themselves, slight variation in electrode placement could have considerable effect on the relative amplitude of signals. Therefore, comparisons have been made only among different conditions in the same preparation. Nevertheless, the general type of information, though not necessarily the exact values, has been obtained in all animals studied. With the exception of humans chewing gum, the normal process of mastication does not deal with a uniform bolus. It is generally agreed (Ahlgren, 1966; Møller, 1966) that otherwise there is great individual variation in the process. Schaerer and Stallard (1965) used a computer of average transients to analyze EMG activity occurring in humans while chewing bread. Each subject chewed 150 small slices of bread, drinking one cup of beverage after every ten slices. Radio transmitters built into the natural teeth of the subject recorded tooth contact; the radio signal resulting from maximal tooth contact was used as one triggering point for computation. After the first five strokes, continuing summation was used for 1,500 consecutive strokes, utilizing several different triggering points. Isotonic and isometric phases of the stroke are separated by the maximal intercuspal position. By playing the tape both forward and backward, this point could be used to try to find a possible average pattern for these two phases of the stroke. The activity for both phases produced "a

complete smearing" of the EMG signal with increasing number of bursts analyzed. They conclude, "the varying mandibular movements and their accompanying high variation in numbers and phase of motor unit recruitments during mastication prevent the quantitation of masticatory EMG response by averaging through analog summation even if related to the same mandibular position". This was due partly to the changing properties of the bolus and partly to the large intra-individual differences in chewing a standard quantity of food. It might almost be said that few people chew exactly the same way twice.

To minimize such differences, Ahlgren and Møller employed a large number of subjects, selected for analysis only those EMG bursts which appeared uniform, and processed the resulting data with a computer. Møller used only the first five or six chewing strokes, that is, those in which the bolus is most uniform.

Rats are similarly variable in their chewing patterns. This was especially obvious with the small uniform pellets. Only data on molarization is presented. Areas of uniform patterns were chosen from two or three complete eating cycles; that is, from biting off a bolus (or ingesting a small pellet), through to its subsequent reduction. The next eating cycle would begin with biting off the next piece of food or putting the next pellet into the mouth.

V. RESULTS

A. *Introduction*

Figure 11 presents two of the original observations which led to this study. Both are from an animal with a single chronic multiunit electrode in Mes V. A shows the two patterns observed as the animal chews a pellet of the standard rat diet, called "large pellet" hereafter. The brain activity associated with incisions was longer in duration and smaller in amplitude than molarization. This has been a consistent finding. B is the result of putting a microphone into the cage with the animal while he chews a large pellet. The audio bursts are the sounds made as the rat bites off a piece of the hard food with his incisors. Although the microphone did not pick up the sound of molarization, it was clear from visual observation that the activity being recorded from Mes V occurred while the jaw closing muscles were actively contracting. An even greater difference between the records of incision and molarization is seen in Figure 12. In both A and B, the upper trace is from the bipolar multiunit electrode in rat 30, while the lower trace is the audio record. Here the activity in Mes V from incision is so slight as to be almost lost in the background.

B. *Experimental Procedure*

The mesencephalic nucleus is known to contain primary cell bodies of Ia muscle spindle fibers and tooth receptors. It

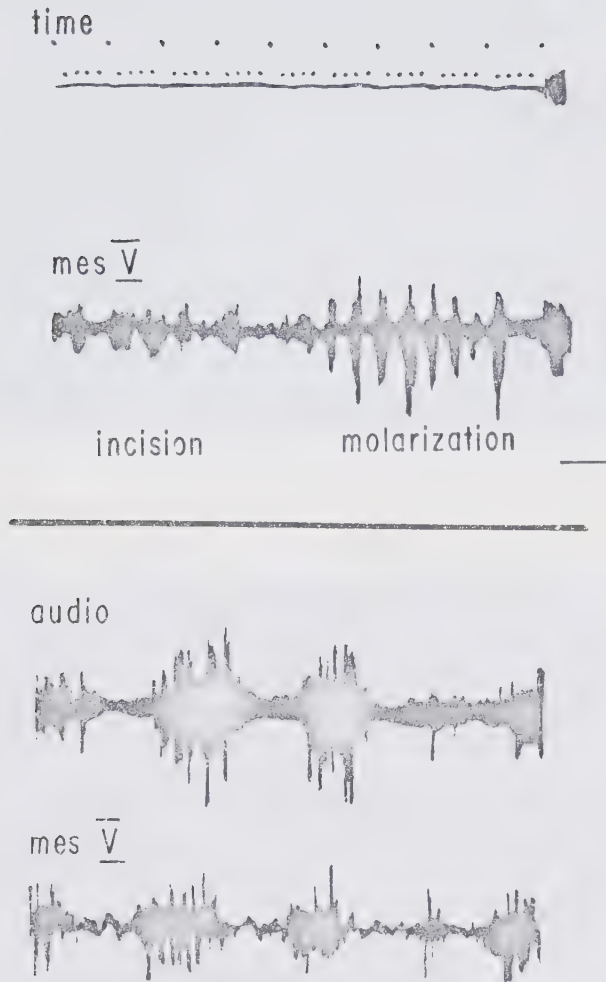


Figure 11. Rat 1: A. Mes V recording of incision, molarization.
Horizontal calibration = 0.5 sec
Vertical calibration = 0.5 mv

B. Top: Audio - "crunch" of large pellet.
Bottom: Mes V recording of incision.

Horizontal calibration = 0.1 sec
Vertical calibration = 0.5 mv

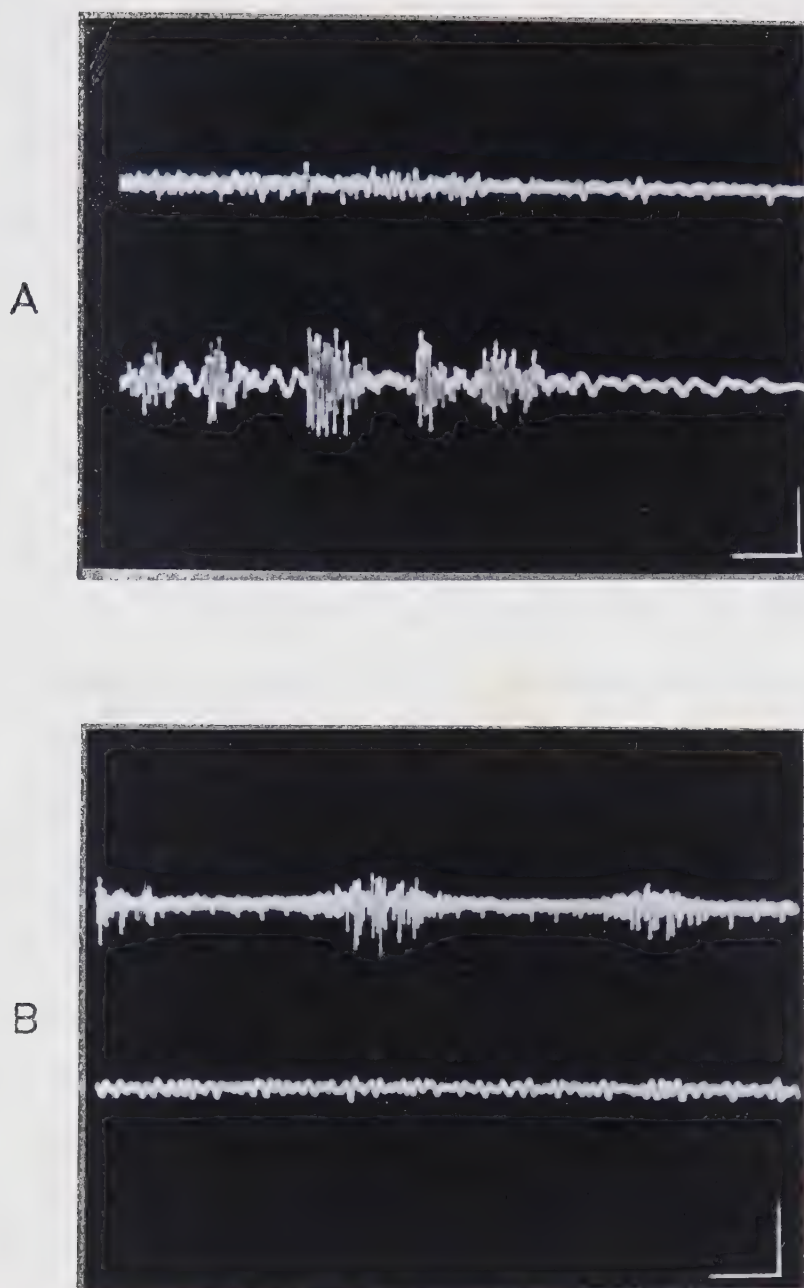


Figure 12. Rat 30. A. Incision B. Molarization.

Horizontal calibration = 20 msec
Vertical calibration = 0.05 mv

Top: Mes V
Bottom: Audio

may contain soma of secondary spindle afferents and of the Ib fibers from Golgi tendon organs, though there is some disagreement on this point. Clearly it was necessary to correlate activity in Mes V with the activity of the muscles of mastication in order to decide what these traces might mean. Therefore, of the twenty-five subjects studied with chronic Mes V electrodes, eleven were also fitted with pairs of bipolar EMG electrodes in masseter and/or digastric muscles. One Mes V animal was also equipped with the jaw movement transducer. An additional nine subjects were used for EMG studies, of which four were fitted with the jaw movement transducers. Four of these animals, including the animal shown in Figure 3A, wore bipolar EMG electrodes in temporalis, masseter, and digastric muscles. Although no combination of Mes V with temporalis was included, it was felt that nearly the same information could be obtained from comparing those experiments having all three muscles represented with the studies of Mes V against masseter and/or digastric.

Table I presents the records obtained for the five types of food tested. "Large pellet" is a piece of standard rat food eaten daily by the animals. These pellets are very hard and the animal makes quite a loud "crunch" as he bites pieces off for further chewing. Usually the pellet would be held in both paws during the entire process, but sometimes an animal would put it down and continue chewing as he moved around the cage, returning to bite off another piece and then resuming his general explorations while he finished it. "Small pellets" are the comparatively tiny

TABLE I. Summary of records obtained for each food studied. Numbers represent subjects receiving a particular treatment.

	Mes V	Temporalis	Masseter
Large pellet	17	3	11
Small pellet	15	4	9
Bread	7	3	8
Chocolate	4	-	3
Pudding	2	2	3

Digastric	Coils	Audio
8	5	8
9	3	-
6	4	-
1	-	-
2	2	-

Noyes precision food pellets (4.0 mm × 3.3 mm × 45 mg) often used as rewards for psychology experiments. Many rats eat these one at a time, but others upset such nice experimental arrangements by stockpiling several in the cheek and then eating the whole group. The pellets are so small that no incisions are necessary. The chewing process for them is thus a continuous series of molarizations. "Bread" was usually a piece of onion bun, since the animals are particularly partial to it. I have awakened a sleeping rat by opening a plastic-film wrapped onion bun near his cage! On other occasions, plain bread or sweet roll were used. All had the same kind of very soft texture. The rat would usually bite off a bit, finish that, and bite off another small piece, finally licking up all available crumbs. "Chocolate" refers to a small piece of solid chocolate (Cadbury Dairy Milk Chocolate). This was fairly hard compared to the bread. Sometimes the animals only licked it rather than actually eating it and these records were disregarded. Finally, "pudding" was included since the animals appeared to lap it up more than actually "chew" it in the normal sense (Jolly canned pudding, either chocolate or vanilla).

Before each recording session, the animal was fasted for 18 to 24 hours; water was always available. He was held carefully in a towel while the recording lead was attached to the head assembly; then he was lowered into the observation cage and allowed to explore it while the overhead carrier for the leads was adjusted and tape recorder gains were set. Usually the animals performed best in a darkened room, so at this stage the lights were

turned out. One test food was placed in the cage. Before starting to eat, the animal would almost always clean his head and paws. Very little of this activity appeared in the brain recording, unless the animal actually tugged at something with his mouth. Thus, the EMG trace would show jaw closing quite often when Mes V was inactive. This observation has been made many times. Unfortunately, no picture is available since the tape was started only when the animal actually began to eat. The rat would be allowed to finish one type of food before another was given, with the exception of the large pellet. If this were offered first, he might be satisfied with it alone, becoming more interested in the recording equipment and observers than in his food after his original hunger was satisfied. Therefore the pellet was removed after a short time unless it was the last food type to be tested in the session.

C. *EMG Studies*

Figure 13 shows the normal pattern of molarization in temporalis, masseter and digastric muscles while the subject eats a large pellet. In Figure 14, such signals have been full-wave rectified and passed through a Paynter filter. Figure 15 shows the normal molarization of small pellets and of bread. A summary of patterns for large and small pellets, bread and pudding appears in Table II. All of this information was from Rat 19, the animal pictured in Figure 3A. Similar patterns were obtained in studies

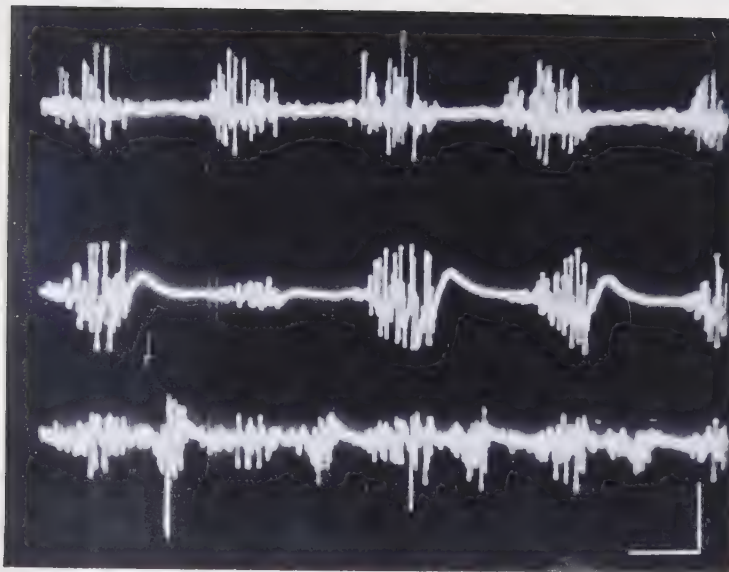


Figure 13. Rat 19: Molarization of large pellet. Horizontal calibration = 0.1 sec.

Top: Temporalis, vertical calibration = 0.2 mv.
Middle: Masseter, vertical calibration = 1.2 mv.
Bottom: Digastric, vertical calibration = 0.7 mv.

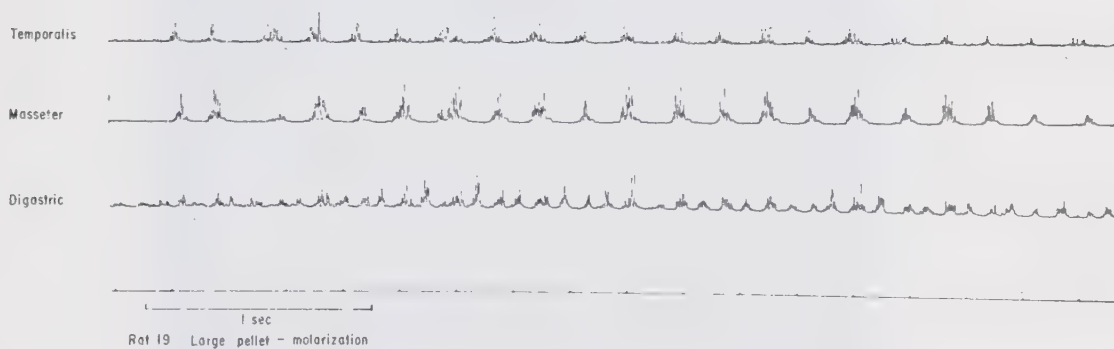


Figure 14. Rat 19: Large pellet molarization, integrated record.

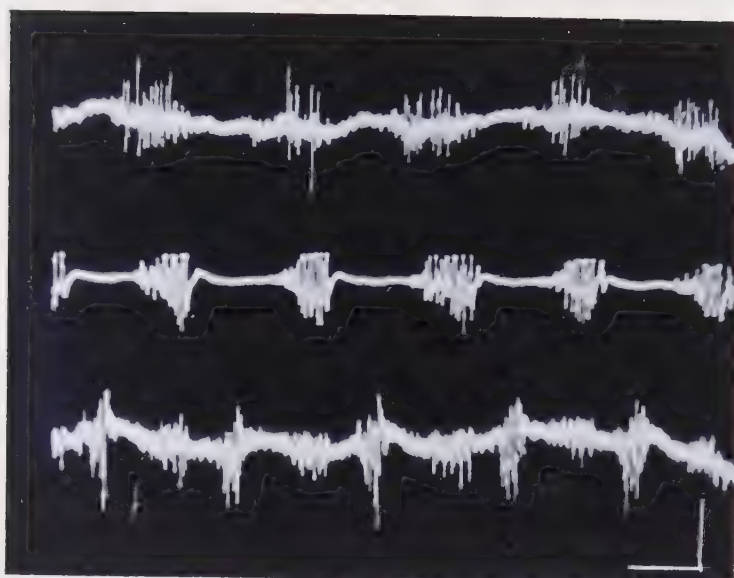


Figure 15. A. Rat 19 eating small pellets.

Top: Temporalis, vertical calibration = 0.21 mv.

Middle: Masseter, vertical calibration = 1.2 mv.

Bottom: Digastric, vertical calibration = 0.29 mv.

Horizontal calibration = 0.1 sec.

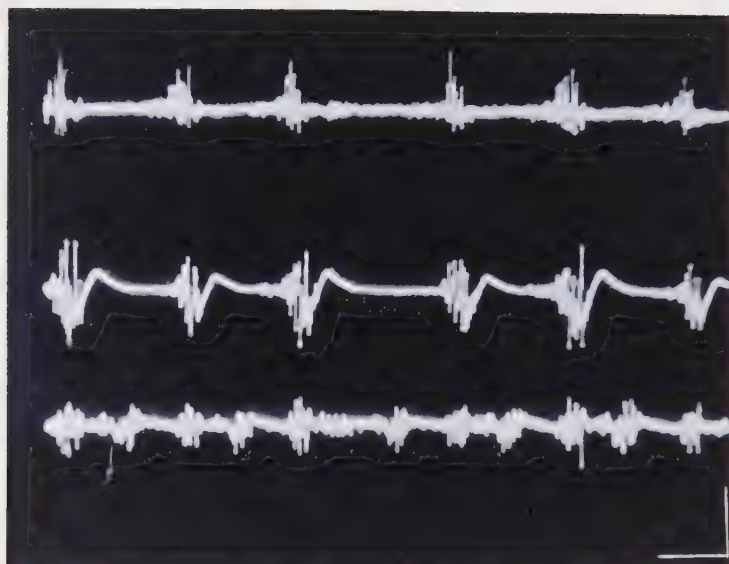


Figure 15. B. Rat 19 eating bread.

Top: Temporalis, vertical calibration = 0.21 mv.

Middle: Masseter, vertical calibration = 0.6 mv.

Bottom: Diaphragm, vertical calibration = 0.72 mv.

Horizontal calibration = 0.1 sec.

TABLE II. EMG parameters for three muscles and four food types - Rat 19.

		Cycle time	Masseter duration	Masseter amplitude	Onset of Temporalis
Large pellet	\bar{X}	180 msec	98.5 msec	0.443 mv	-41 msec
	S	29.0	14.8	0.235	23
	C.C.I.	180±12.5 msec	98.5±6.msec	0.443±0.101 mv	-41±10 msec
Small pellet	\bar{X}	189 msec	101 msec	0.320 mv	-40 msec
	S	31	17	0.115	19
	C.I.	189±13 msec	101±7 msec	0.320±0.048 mv	-40±8 msec
Bread	\bar{X}	157 msec	78 msec	0.447 mv	-25 msec
	S	18	16	0.094	18
	C.I.	157±8 msec	78±7 msec	0.447±0.039 mv	-25±8 msec
Pudding	\bar{X}	95 msec	43 msec	0.059 mv	
	S	12	17	0.017	
	C.I.	95±5 msec	43±7 msec	0.059±0.007 mv	

\bar{X} = mean

S = standard deviation

C.I. = 95% confidence interval = $\bar{X} \pm (t \text{ probability at the 5\% level for } N-1 \text{ degrees of freedom}) (S_{\bar{X}})$

$S_{\bar{X}}$ = standard error of the mean = $\frac{S}{\sqrt{N-1}}$

Temporalis duration	Temporalis amplitude	Onset of digastric	Primary Digastric duration	Primary Digastric amplitude
124 msec	.039 mv	-92 msec	60 msec	0.061 mv
22	.018	28	12	0.023
124±9 msec	0.039±0.007 mv	-92±12 msec	60±5 msec	0.061±0.009 mv
134 msec	.045 mv	-74 msec	55 msec	0.091 mv
36	.005	13	11	0.026
134±15 msec	0.045±0.002 mv	-74±6 msec	55±5 msec	0.091±0.011 mv
82 msec	.069 mv	-72 msec	53 msec	0.089 mv
19	.023	15	14	0.025
82±8 msec	0.069±0.009 mv	-72±6 msec	53±6 msec	0.089±0.011 mv

of Rats 20, 21 and 22; like Rat 19, they all had bipolar EMG electrodes in temporalis, masseter and digastric. The information was also confirmed for the masseter-digastric combination in Rats 7, 8, 10, 13, 14, 15 and 26. Cycle time is time between beginning of masseter activity and onset of the next masseter burst. Onset of activity for temporalis and digastric muscles is expressed in relation to the beginning of the masseter EMG activity.

Both masseter and temporalis are active only once during each cycle of closing and opening the mouth during chewing. Both are jaw elevators and contract as the mandible is raised, fitting the definition of "primary" activity given by Møller (1966). They do not exhibit any "secondary" activity (in this case, activity in an elevator appearing during opening; see definition, p. 36). For the purpose of this discussion, it will be stipulated that "primary" activity in digastric refers to that occurring between the periods of masseter activation. Therefore, "secondary" activity in digastric will be activity which is concurrent with that in masseter.

Secondary digastric activity in Rat 19 appears very similar to the activity in masseter, and for this reason it was not included in Table II. This suggests that digastric and masseter muscles do not contract together, but instead the apparent secondary activity in digastric is actually "crosstalk", the registration of activity from one muscle by electrodes placed in another. Examination of records from other animals (and also of various characteristics of this animal's record, mentioned in the following pages) does not

support this conclusion. Figure 16A shows a scattergram of secondary digastric amplitude plotted against masseter amplitude, taken from a record of Rat 14 chewing small pellets. The Pearson product moment correlation coefficient calculated from these values was +0.45. Although there is a positive relationship between the two variables, this degree of correlation is not significant at either the 1% or the 5% confidence level. Therefore the null hypothesis, that there is no significant correlation between secondary digastric amplitude and masseter amplitude, is not rejected.

From Table II, the chewing rates for the different food types are:

Large pellet	5.5 Hz
Small pellet	5.3 Hz
Bread	6.4 Hz
Pudding	10.5 Hz

Thus, this animal chews the large pellet, once it is in his mouth, at about the same speed as the small ones, but bread is chewed 10% more quickly and pudding is almost twice as fast.

Pudding is a rather special case, perhaps comparable to the bread and milk used in Hiemäe's study (1967). Note that

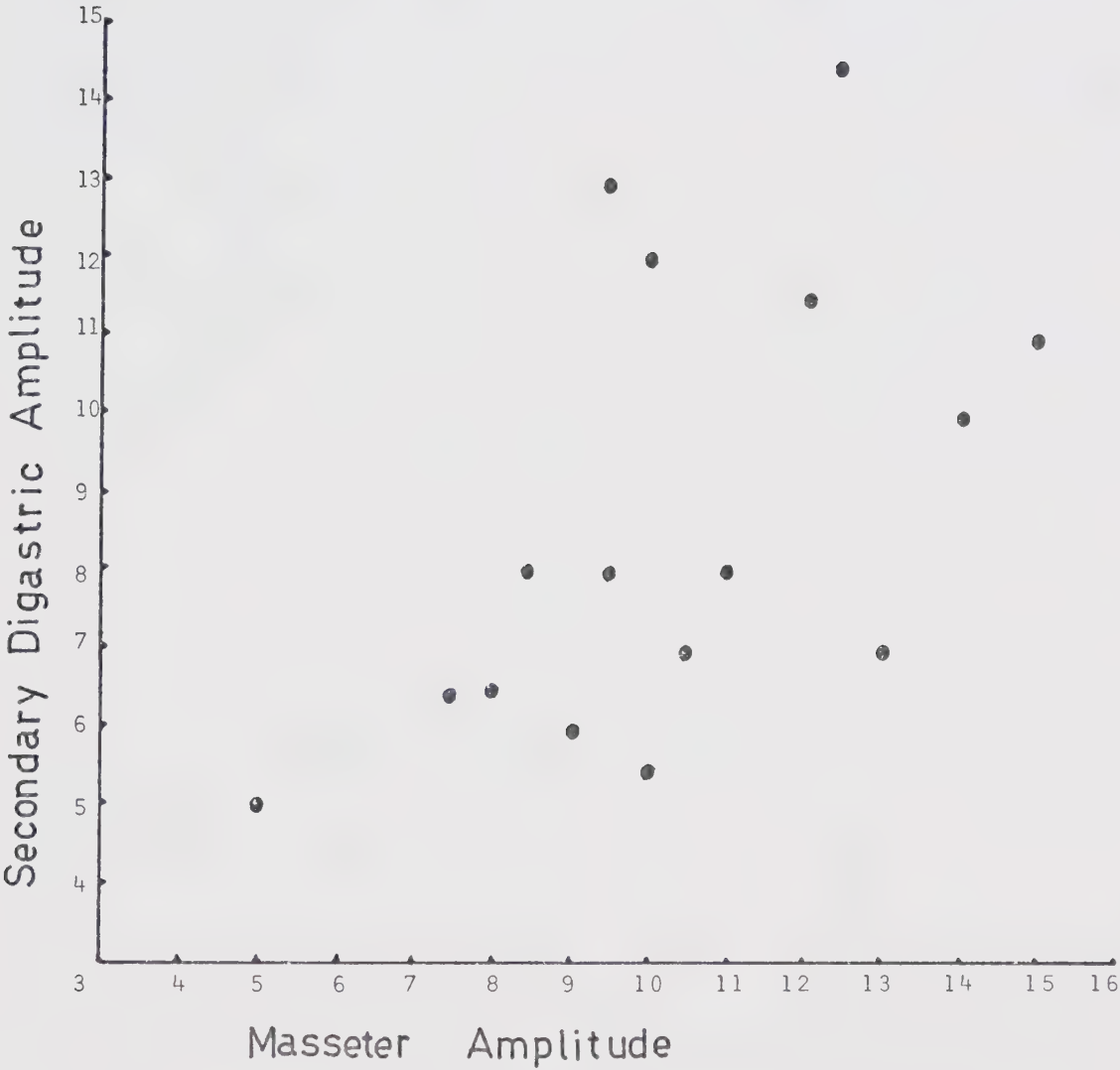


Figure 16A. Amplitude of secondary digastric EMG activity plotted against masseter EMG amplitude. Both scales are plotted in arbitrary units. (From record of Rat 14 eating small pellets.)

Table II presented only those parameters dealing with activity in masseter. The reason for this is clear from Figure 16B, a record of Rat 19 eating pudding. Only the activity in masseter occurred in well-defined cycles. Both temporalis and digastric exhibited almost continuous low level activity. Even in masseter the peak of activity in the average integration traces was 7.5 times smaller than that found for hard food.

Inspection of Table II indicates that activity in masseter, for example, lasts about the same amount of time for large and small pellets, while it is decreased by 12% for bread and by 43% for pudding. However, if duration of activity is expressed in terms of cycle time, the results are rather different:

% OF CYCLE TIME

	Masseter	Temporalis	Digastric/"Primary" Activity
Large pellet	55%	69%	33%
Small pellet	53%	71%	29%
Bread	50%	52%	34%
Pudding	45%	-	-

Here it appears that masseter and digastric are active the same relative amount of time for each different kind of food. When bread is being chewed, temporalis is only 70% as active as for the two kinds of pellet.

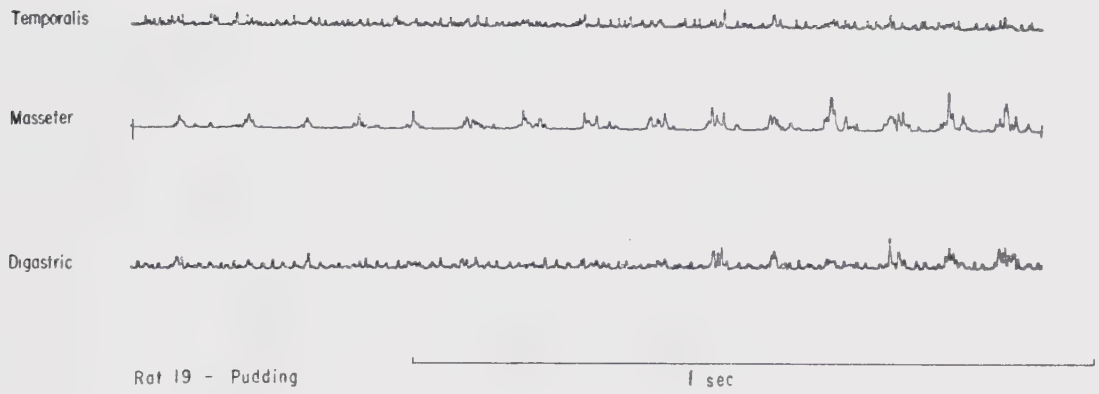


Figure 16B. Rat 19 eating pudding, integrated record.

According to the information of Table II, temporalis normally leads masseter for molarization of three food types.

Expressed in terms of cycle length:

	Lead time of Temporalis	Lead time of Digastric
Large pellet	-23%	-51%
Small pellet	-21%	-39%
Bread	-16%	-46%

Therefore, when cycle time is measured from the beginning of activity in masseter to beginning of next masseter activity, digastric primary activity (jaw opening) occurs after 50 to 60% of the cycle while temporalis leads masseter by 20%. Maximum amplitudes were nearly the same for large pellet and bread in masseter and bread and small pellets in digastric. All are different only in temporalis where the trend seems to follow the inverse of the degree of hardness in the series: that is, large pellet requires less activity than does small pellet than does bread.

Clearly there is a great deal of variability shown in the results and the most variable is onset of activity in temporalis. Amplitudes of activity in all three muscles are also extremely variable.

Only molarization patterns have been considered so far. Figures 17 and 18 show incision for large pellet and bread, respectively. As mentioned earlier, there is no incision phase for the small pellets, nor can such a phase be distinguished for eating

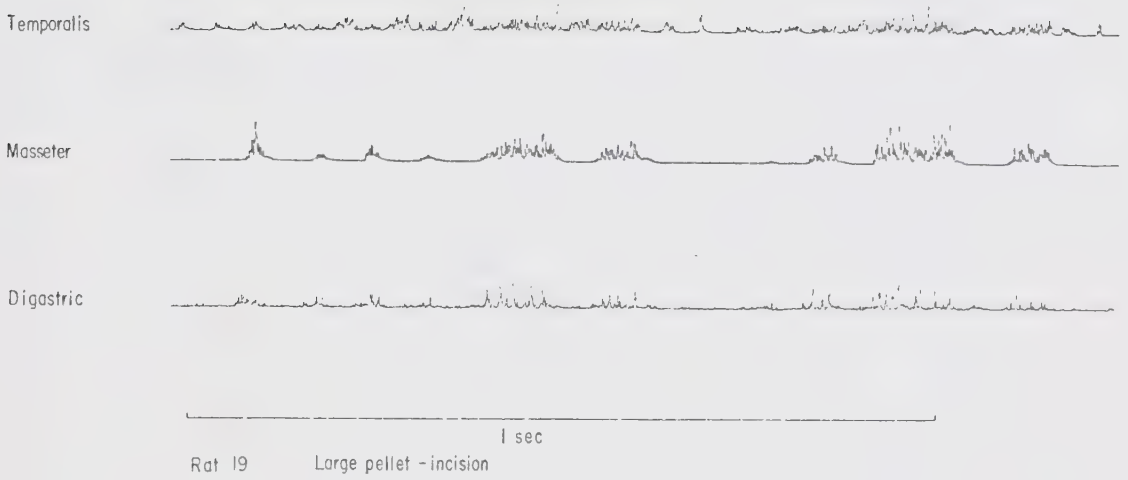


Figure 17. Rat 19: Incision of large pellet, integrated record.

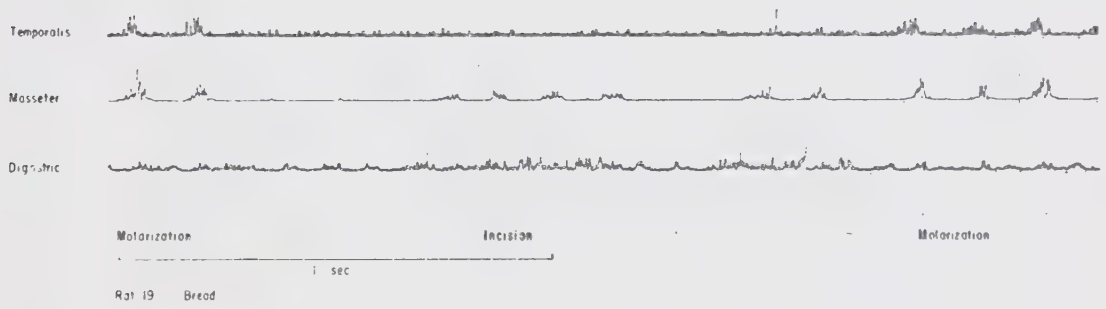


Figure 18. Rat 19: Bread - molarization and incision, integrated record.

pudding. Figure 17 presents the incisions which immediately preceded the large pellet molarizations of Figure 14. Note the lengthened duration of activity in masseter, approximately twice normal. Generally, amplitude is considerably less than usual, though the example shows them to be within the normal range. Although temporalis leads masseter by an average of 40 msec in molarization, on incision the two muscles work together. Activity in the digastric muscle during incision is virtually continuous, with much greater independence of EMG activity in masseter and digastric than appeared in the molarization record. This would seem to support the notion of co-contraction in the two muscles.

The pattern of muscle activity for incision of bread is shown by Figure 18. Two molarization cycles are followed by six incision cycles (as counted from the activity in masseter); the last four cycles again show molarization. Activity in masseter is regular, though diminished considerably in amplitude. However temporalis displays a low level of continuous activity throughout, in contrast to the bursts seen in large pellet incision. Digastric activity is nearly continuous during masseter activity; however, when masseter is inactive, separate bursts in digastric are clear. Here again, although it is quite possible that there might be "crosstalk" between the two pairs of electrodes when masseter and digastric are active simultaneously, this appears less likely considering the independent activity demonstrated in this segment.

D. *Relationship of Jaw Position and EMG Activity*

To complete the description of EMG activity in the masticatory muscles of the rat, it would be useful to relate EMG activity to relative jaw position. This was done with Rats 18, 32, 33 and 34. Typical molarization results for Rat 32 eating large pellet, small pellet, bread and pudding are shown in Figures 19A, 19B, 20A and 20B, respectively. The top trace represents jaw movement in all cases, with jaw closing signified by downward movement of the trace. The middle trace is the bipolar masseter EMG while the lower trace is the integrated EMG. Note the occurrence in the masseter EMG of a silent period for every type of food except pudding. Maximum EMG amplitude could come either before or after the silent period, though it usually came afterwards.

Figure 21 shows Rat 32 eating a large pellet. A fourth trace for the audio record of the "crunch" of incision has been added below the others. The difference in amplitude normally found between incision and molarization when chewing the large pellet is clearly illustrated by Figure 21A. It can be seen that there may be some sound generated before there is evidence of masseter activity. This might support the idea that elastic rebound is responsible for the early part of jaw closing (Ahlgren, 1966). On incision, masseter and temporalis work synchronously. Therefore the normal lead of temporalis in molarization cannot account for this early sound in the audio record. A series of such incisions is presented in Figure 21B. For both pictures, the horizontal calibration line represents 200 msec, while the calibration for the earlier series

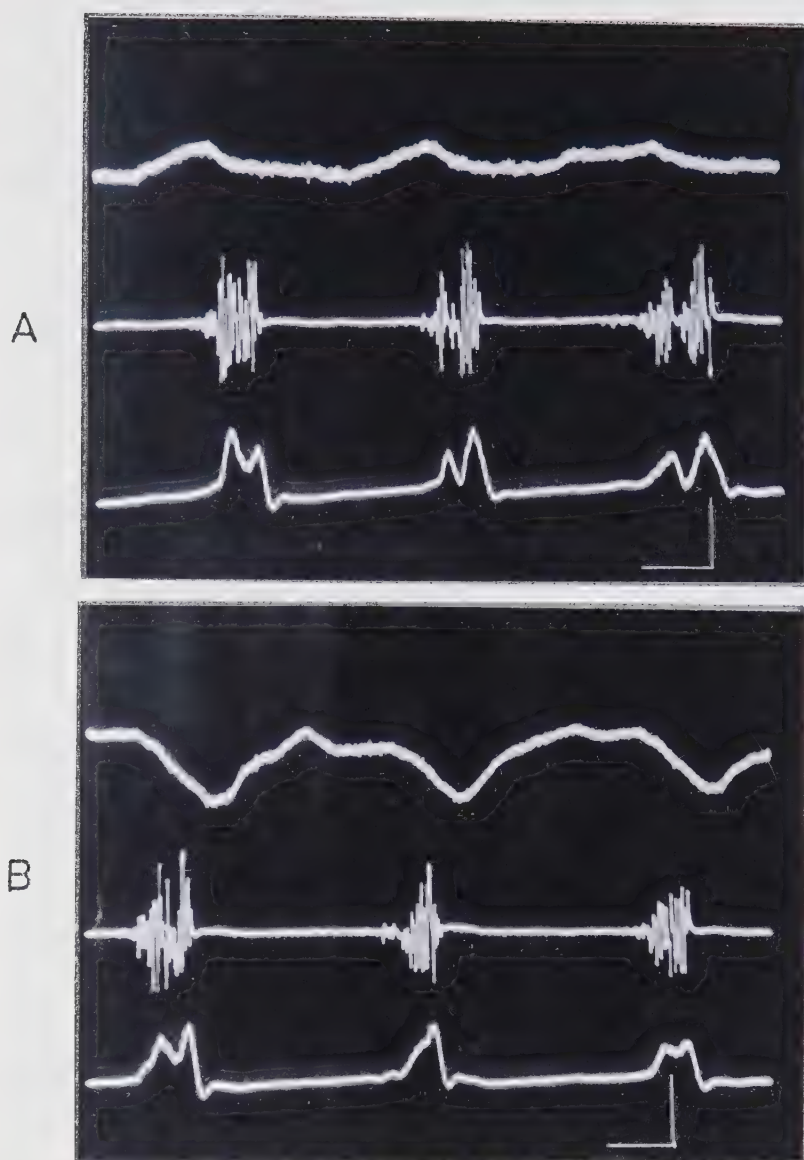


Figure 19. Rat 32: A. Large Pellet. B. Small Pellets.

Top: Transducer.*

Middle: Masseter EMG, vertical calibration = .78 mv.

Bottom: Integrated EMG, vertical calibration = .39 mv.

Horizontal calibration = 50 msec.

* Sensitivity of carrier amplifier was set at 200 μ strain/div for Fig. 19, 20, and 21.

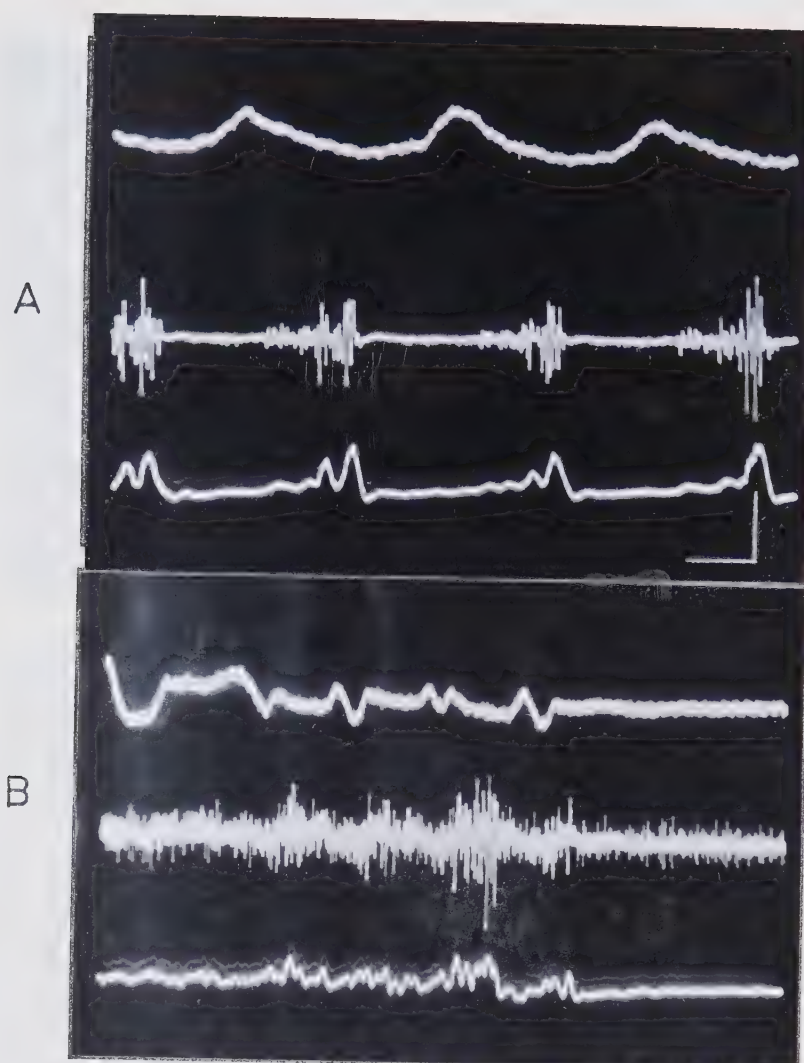


Figure 20. Rat 32: A. Bread.

Top: Transducer.

Middle: Masseter EMG, vertical calibration
= .35 mv.

Bottom: Integrated EMG, vertical calibration
= .18 mv.

B. Pudding.

Top: Transducer.

Middle: Masseter EMG, vertical calibration
= .027 mv.

Bottom: Integrated EMG, vertical calibration
= .014 mv.

Horizontal calibration = 50 msec.

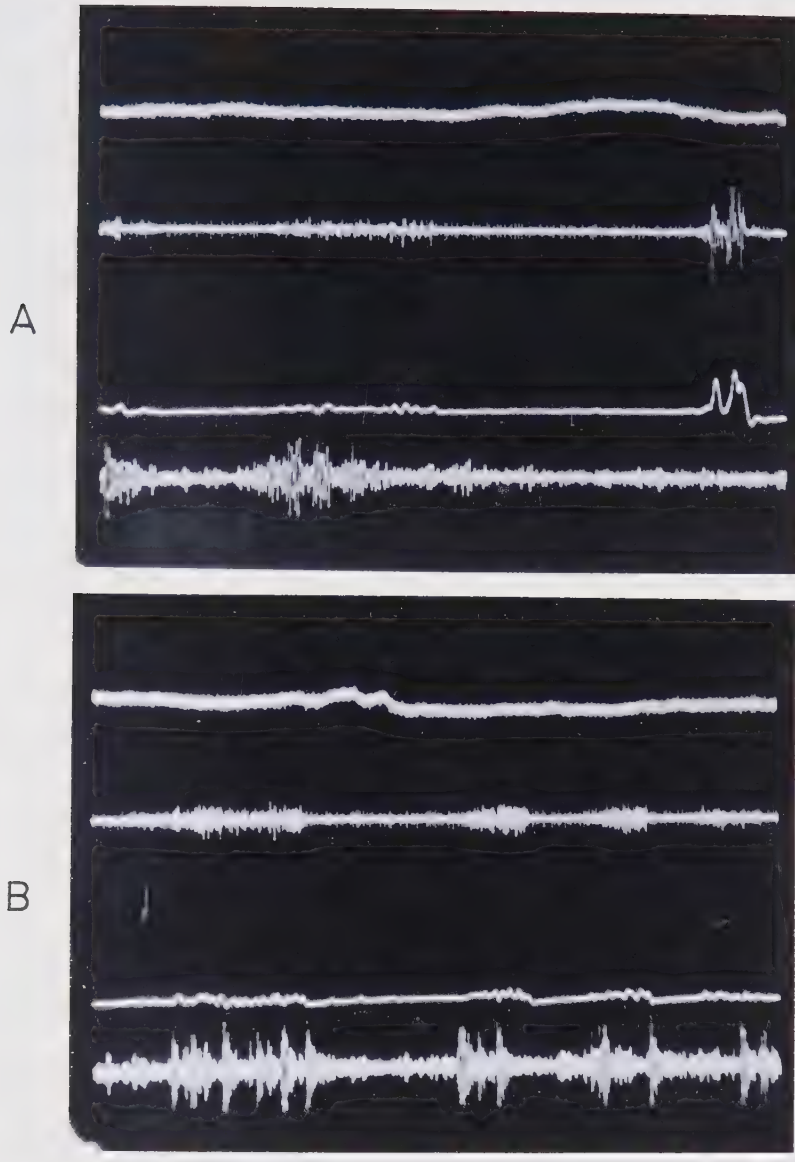


Figure 21. Rat 32: Large Pellet A. Incision, molarization.
B. Incision.

- A. Transducer.
- B. Masseter EMG, vertical calibration = .26 mv.
- C. Integrated EMG, vertical calibration = .13 mv.
- D. Audio, vertical calibration = .5 v.

Horizontal calibration = 200 msec.

was 50 msec. The sensitivity of the carrier amplifier was not changed for the sequence of Figures 19A, 19B and 20A. Therefore the movement of the top trace may be taken as a rough guide to the degree of opening and closing which occurred. (This is not true for EMG amplitude, since the gain for masseter activity was lower for the large pellet; gains for bread and small pellet were the same and relative activity can be estimated.) Figures 20B and 21A and B were taken on another day, though carrier amplifier sensitivity was again set at 200 μ strain/div.

Studies by Ahlgren (1967, 1969) have indicated that the silent period seen in masseter and temporalis during chewing in human coincides with tooth contact and that the occlusal phase (that is, the time during which the teeth are in the intercuspil position) "corresponds to the interval between the 'occlusal silent period' in the EMG and the termination of the EMG pattern of the masticatory cycle" (Ahlgren and Öwall, 1970).

Table III presents the relationship of jaw position to EMG activity in masseter. Conditions examined are chewing large pellet, small pellet and bread.

Chewing rates for this animal (Rat 32) were:

Large pellet	5.3 Hz
Small pellet	4.9 Hz
Bread	6.3 Hz

If the closing phase is defined as from the beginning of closing movement shown by the transducer to the silent period in the EMG, and the occlusal phase is defined as from silent period to termination

TABLE III. Relationship of jaw position to EMG activity in masseter
- Rat 32.

		Cycle Period	Masseter Duration
Large pellet	\bar{X}	187 msec	38 msec
	S	28	8
	C.I.	187±12 msec	38±3.5 msec
Small pellet	\bar{X}	205 msec	46 msec
	S	23	14
	C.I.	205±10 msec	46±6 msec
Bread	\bar{X}	158 msec	75 msec
	S	9	25
	C.I.	158±5 msec	75±12 msec

\bar{X} = mean

S = standard deviation

C.I. = 95% confidence interval = $\bar{X} \pm$ (t probability at the 5% level
for N-1 degrees of freedom) ($S_{\bar{X}}$)

$S_{\bar{X}}$ = standard error of the mean = $\frac{S}{\sqrt{N-1}}$

Onset of Closing to Onset of EMG	Onset of EMG to Silent Period
16 msec	19 msec
22	6
16 ± 10 msec	19 ± 3 msec
6 msec	25 msec
7	12
6.2 ± 3 msec	25 ± 6 msec
14 msec	49 msec
7	4
14 ± 5 msec	49 ± 3 msec

of masseter EMG activity, then the duration of closing, occlusal and opening phases are:

	Closing	Occlusion	Opening
Large pellet	35 msec	19 msec	133 msec
Small pellet	31 msec	21 msec	153 msec
Bread	63 msec	26 msec	69 msec

or as a percentage of cycle time:

	Closing	Occlusion	Opening
Large pellet	19%	10%	71%
Small pellet	15%	10%	75%
Bread	40%	16%	44%

Thus the time relations of large and small pellet chewing are rather similar. An examination of Figure 19A and 19B, however, leaves one unconvinced that the processes are quite the same. The rapid jaw movement as the muscle contracts for the small pellet suggests that the teeth bite quickly through the food; in fact, some closing force may be present after the "occlusal phase" in both of these types of chewing. The pellet chewing pattern seems to take the following sequence: 1) jaw opens from previous cycle; 2) it closes just enough to hold a particle of food between the teeth (and this phase required no muscle activity, it was simply an elastic rebound effect); 3) force slowly builds up. Then either the food suddenly "gives", with force lasting beyond the EMG activity (small pellet) or the force simply increases with rather slow crushing effect and the jaw opens slightly for the next attack (large pellet). Thus the small pellet

chewing pattern is more ballistic. The process of chewing bread is quite symmetrical, with the closing and occlusal phases summing (56% of cycle) to give the slightly skewed effect seen in 20A. Here again, the force (as indicated by closing movement) continues beyond the EMG. Smooth continuous closing is followed by somewhat more rapid opening. The record of eating pudding (Figure 20B) shows a very jerky movement which is difficult to correlate with the EMG. Amplification of masseter EMG record is ten times greater in Figure 20B (pudding) than in Figure 20A (bread).

E. *Correlation of Activity in the Mesencephalic Nucleus V with That in the Muscles of Mastication*

How is activity in the mesencephalic nucleus of the trigeminal nerve related to activity in the muscles of mastication? In Figure 22 from Rat 9, the top trace is Mes V activity, while the lower trace is the masseter EMG. Mes V activity (above) and digastric activity (below) are shown in Figure 22B, from Rat 12. Both animals were eating a large pellet. Activity of masseter is entirely contained within that of Mes V while the burst of secondary activity in digastric starts after the onset of Mes V activity and lasts somewhat longer.

A comparison of Mes V and masseter activity for three types of food appears in Table IV. The chewing rates shown are:

Large pellet	5.4 Hz
Bread	6.4 Hz
Chocolate	6.5 Hz

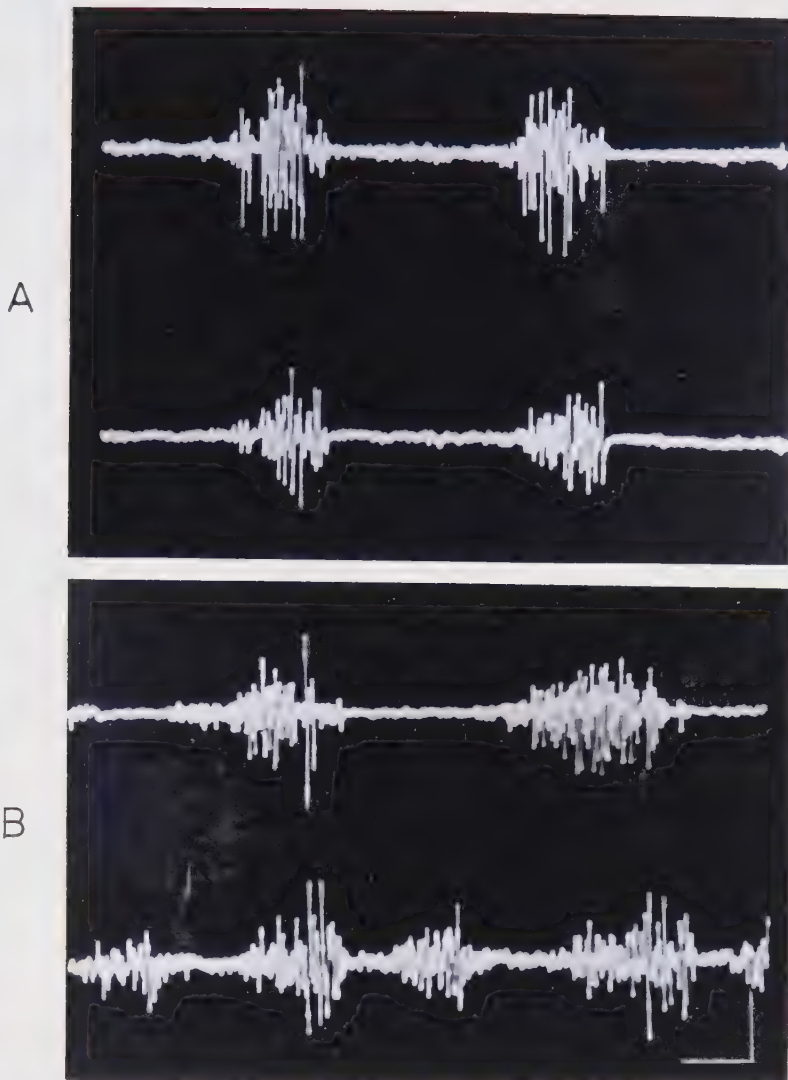


Figure 22. Large Pellet. A. Rat 9
 Top: Mes V, vertical calibration = 0.25 mv.
 Bottom: Masseter, vertical calibration = 0.4 mv.

B. Rat 12
 Top: Mes V, vertical calibration = 0.65 mv.
 Bottom: Digastric, vertical calibration = 0.35 mv.
 Horizontal calibration = 50 msec

TABLE IV. Relationship of activity in Mes V and masseter - Rat 9.

		Cycle Period	Mes V Duration	Mes V Amplitude
Large pellet	\bar{X}	185 msec	85 msec	.162 mv
	S	18	16	.035
	C.I.	185±8 msec	85±6 msec	.162±.014 mv
Bread	\bar{X}	157 msec	48 msec	.092 mv
	S	9	14	.029
	C.I.	257±4 msec	48±6 msec	.092±.012 mv
Chocolate	\bar{X}	153 msec	67 msec	.108 mv
	S	23	12	.026
	C.I.	153±10 msec	67±5 msec	.108±.011 mv

\bar{X} = mean

S = standard deviation

C.I. = 95% confidence interval = $\bar{X} \pm$ (t probability at the 5% level
for N-1 degrees of freedom) ($S_{\bar{X}}$)

$S_{\bar{X}}$ = standard error of the mean = $\frac{S}{\sqrt{N-1}}$

Onset of Activity in Mes V	Masseter Duration	Masseter Amplitude
-14 msec	77 msec	0.112 mv
18	15.5	.024
-14±7.5 msec	77±7 msec	.112±.010 mv
-4 msec	63 msec	.218 mv
9	11	.077
-4±3.8 msec	63±5 msec	.218±.032 mv
-5 msec	76 msec	.282 mv
9.5	14	.063
-5±4 msec	76±6 msec	.282±.026 mv

As a percentage of the cycle:

	Mes V Duration	Masseter Duration	Onset of Mes V Activity
Large pellet	46%	41%	-7.5%
Bread	31%	40%	-2.5%
Chocolate	44%	50%	-3.3%

Mes V showed activity for a longer time than masseter when chewing a large pellet, a shorter time for both bread and chocolate. Similarly, amplitude of activity in Mes V was over 50% greater for the large pellet than for the other foods. Also, the lead of Mes V activity compared to masseter was greater when chewing hard food. In Table II it was shown that temporalis consistently leads masseter and that this lead is greater for large and small pellets than for bread.

The silent period appearing in the EMG of masseter and temporalis muscles was noted earlier. A similar silent period appears in Mes V (Fig. 23). This shows Mes V-masseter activity in Rat 9 eating a large pellet. In this instance, duration of the silent period is about 10 msec. This is a bit shorter than the 15 msec found under urethane anesthesia in the rat and considerably shorter than the 200 msec duration found under sodium pentobarbital (Thomas, 1972). Evidently the silent period is not always present when pentobarbital is used.

Figure 24 is another example of Mes V/digastric coordination. As before, there are two bursts in digastric for every one in Mes V (or in masseter or temporalis). The so-called primary activity here (that is, the activity occurring between Mes V bursts)

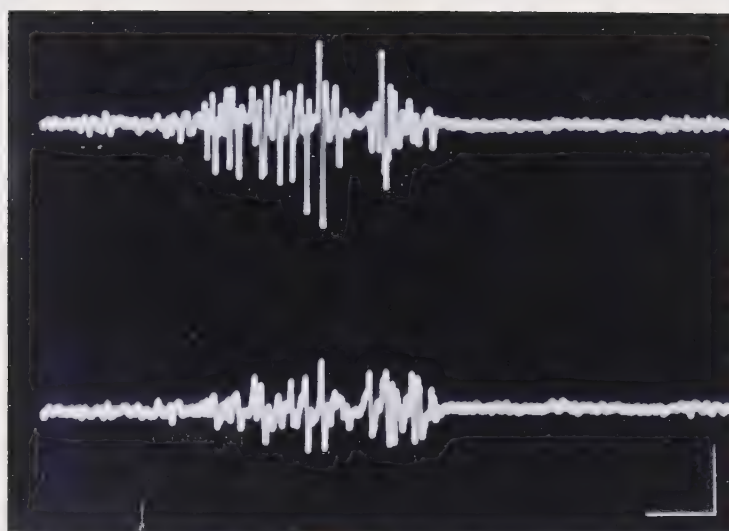


Figure 23. Rat 9: Silent period while chewing large pellet.

Top: Mes V, vertical calibration = 0.26 mv.

Bottom: Masseter, vertical calibration = 0.30 mv.

Horizontal calibration = 20 msec.

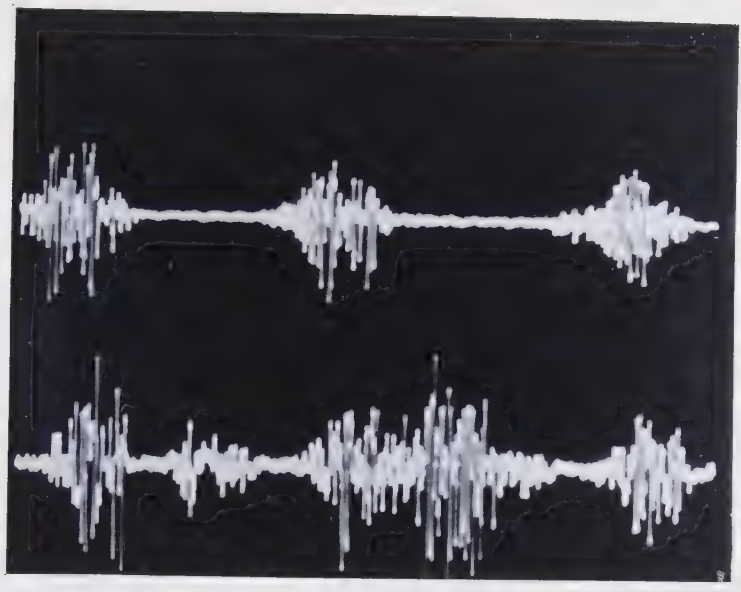


Figure 24. Rat 12 - small pellet.

Top: Mes V, vertical calibration = 0.66 mv.

Bottom: Digastric, vertical calibration = 0.35 mv.

Horizontal calibration = 50 msec.

is considerably smaller than the secondary. But in one place on this illustration these normally separate phases of digastric activity are observed to be continuous. In a chewing sequence of 35 cycles, this aberrant form appeared three times at evenly spaced intervals.

"Chewing" does occur in the decerebrate rat (Thomas, 1969). This kind of activity is shown in Figure 25. The decerebrate animal was placed in a stereotaxic apparatus, kept warm by a warm lamp from above or a hot water bottle beneath. After placing electrodes in Mes V, masseter, and digastric, chewing is produced by touching simultaneously the upper and lower incisors and pressing lightly. This is very much like placing the tip of a finger between his teeth. After a short period of such priming, the lower incisors are brought forward in the normal rat position for incision and the finger feels as if it is being nibbled. Sometimes the finger is removed fairly quickly in expectation of being truly bitten! Parts of such sequences are shown in the EMG record of Figure 25A, and the combined Mes V-EMG record of Figure 25B. In A, digastric activity starts part way through the masseter burst, and reaches its maximum amplitude at about the end of the masseter pattern. In B, digastric may begin either with masseter or later; however the cessation of activity in the two muscles is usually synchronous. The large units shown in Mes V, on the other hand, seem to begin after masseter and may remain active longer. Sometimes digastric activity is separated into two bursts (like normal primary and secondary activity), but this is fairly unusual.

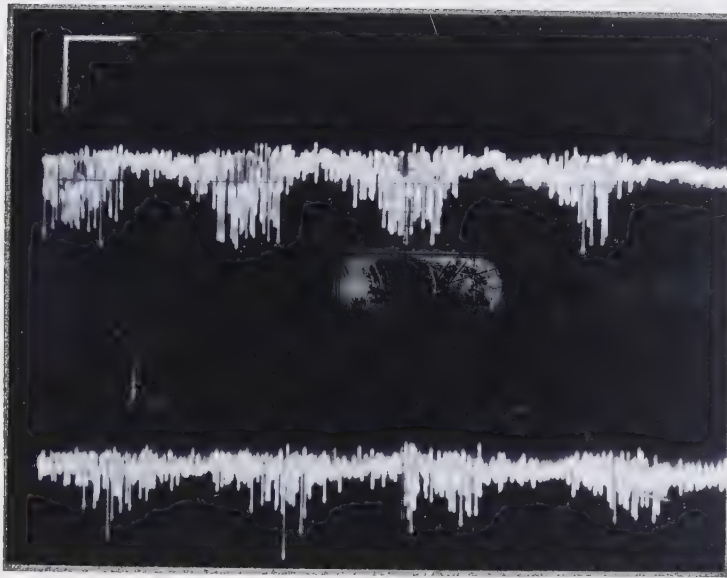


Figure 25. "Chewing" in the decerebrate rat.

- A. Top: Masseter
Bottom: Digastric
Vertical calibration = 0.08 mv.
Horizontal calibration = 50 msec.

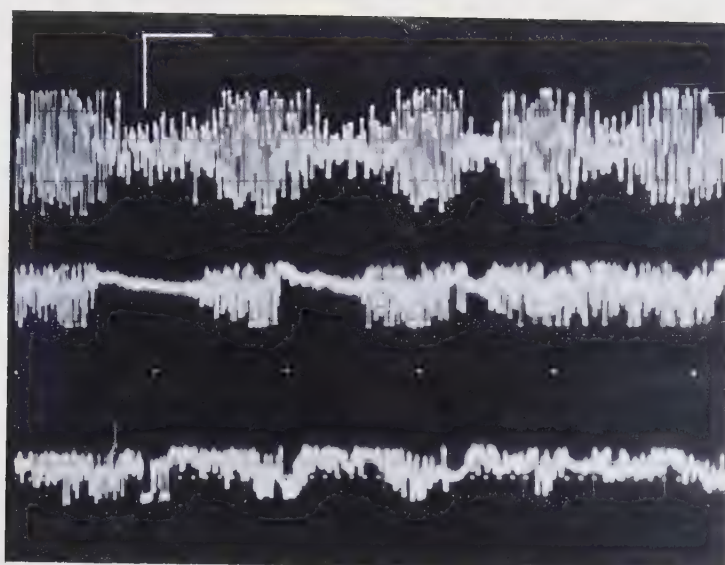


Figure 25. "Chewing" in the decerebrate cat.

- B. Top: Mes V, vertical calibration = 0.1 mv.*
Middle: Masseter, vertical calibration = 0.08 mv.
Bottom: Digastric, vertical calibration = 0.08 mv.

Horizontal calibration = 50 msec.

* All Mes V records from decerebrate animals were made with microelectrodes having 1 μ tip diameter and 2 μ exposed tip length.

A complete record of such a chewing sequence appears in Figure 26. The animal is chewing at about 125 msec per cycle, or 8 Hz.

A similar type of synchronous activity occurs in the normal rat, what I have called the "toothbrushing effect", for lack of a more precise functional explanation (Fig. 27). The muscles work synchronously and there may or may not be Mes V activity at the same time. The animal's entire face trembles but the mouth does not seem to be opening and closing. The rate is about 12 Hz, considerably faster than either normal or decerebrate chewing. Such a pattern may occur either before an animal begins to eat, along with face and paw cleaning, or it may occur after he finishes. A few animals would do this more often, as between courses of a meal.

F. *Evidence for Ia Activity in Mes V, as Recorded in the Chronic Animal*

Mes V contains primary cell bodies of Ia afferents from the muscle spindles and of periodontal mechanoreceptors. There may be secondary spindle and Golgi tendon organ fibers (II and Ib) in addition, though this is less certain. The activity recorded from Mes V cannot be evaluated unless it can be determined which of these different cells are the source(s).

To try to answer this question, animals with chronic multiunit electrodes were tested first for normal chewing responses and second for presence of different types of possible Mes V components. Decerebrate, anesthetized, or tranquilized animals were

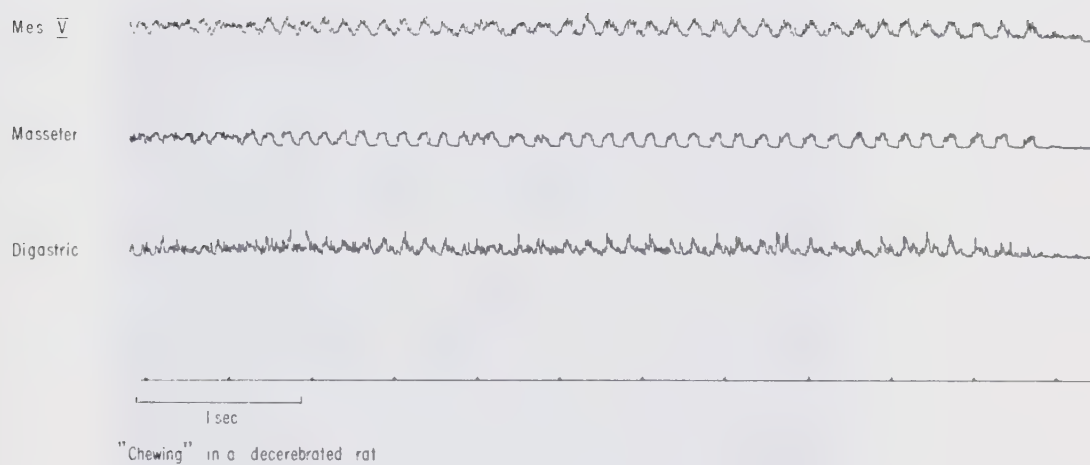


Figure 26. "Chewing" in the decerebrate rat, integrated record.

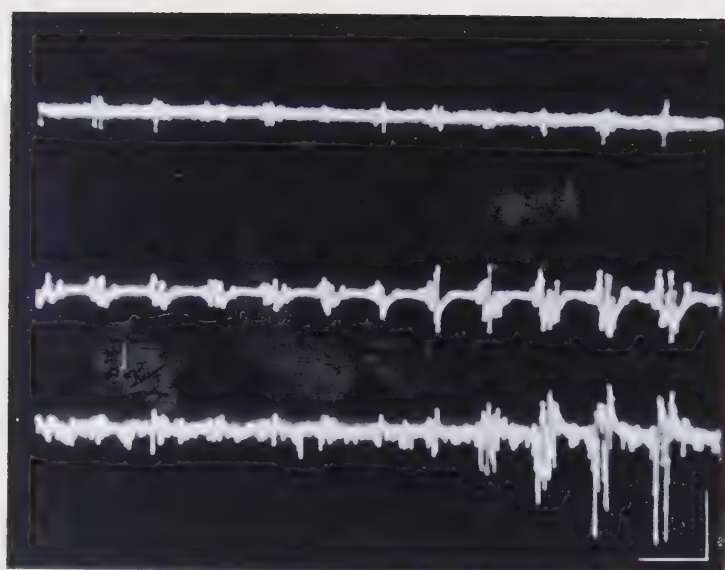


Figure 27. Rat 19: Synchronous 12 Hz "tooth brushing(?)"

Top: Temporalis, vertical calibration = 0.21 mv

Middle: Masseter, vertical calibration = 1.4 mv

Bottom: Digastric, vertical calibration = 1.01 mv

Horizontal calibration = 0.1 sec

used in this part of the study.

Under urethane anesthesia, passive stretch of the jaw elevators by depressing the mandible produces activity in Mes V (Fig. 28A). This is the usual test for muscle spindle activity in the nucleus (Jerge, 1963; Taylor and Davey, 1968). It was also possible to localize specific muscle spindles from which activity was being picked up on the chronic electrodes. For instance, probing masseter with a small wooden probe on one occasion produced best response in the triangle of deep masseter which is not covered by superficial masseter, just below the zygomatic arch. Both ipsilateral and contralateral points were responsive. Although this area was near the TMJ, it was higher than medial pterygoid. Other active points for this electrode position were found on temporalis, but none on digastric. To determine the latency of this response, direct electrical stimulation was applied at 1 Hz, amplitude 100 mv, pulse width 0.5 msec, using a concentric bipolar electrode. Figure 28B shows Mes V reaction due to stimulation of a point in deep masseter; ten successive stimulations are superposed, five using normal polarity of stimulating electrodes and five in which the polarity was reversed. The small size of the muscle involved makes it very difficult to confine the stimulus to a single spindle; therefore the evoked potential shown at the arrow represents the response of several Ia fibers to direct stimulation. The latency of 0.5 to 0.7 milliseconds agrees closely with that found by direct stimulation of the masseteric nerve (Thomas, 1972). No activity was recorded in this particular electrode position during stimulation of the teeth, even when they were forcibly clenched

together. There was a large response when the mouth was stretched open.

Although such results were obtainable with urethane, they could not be repeated under pentobarbital anesthesia. Jaw stretch almost never produced increased Mes V activity under this anesthetic. A response to tapping a tooth could be obtained. This was probably a synchronous spindle discharge due to vibration of the

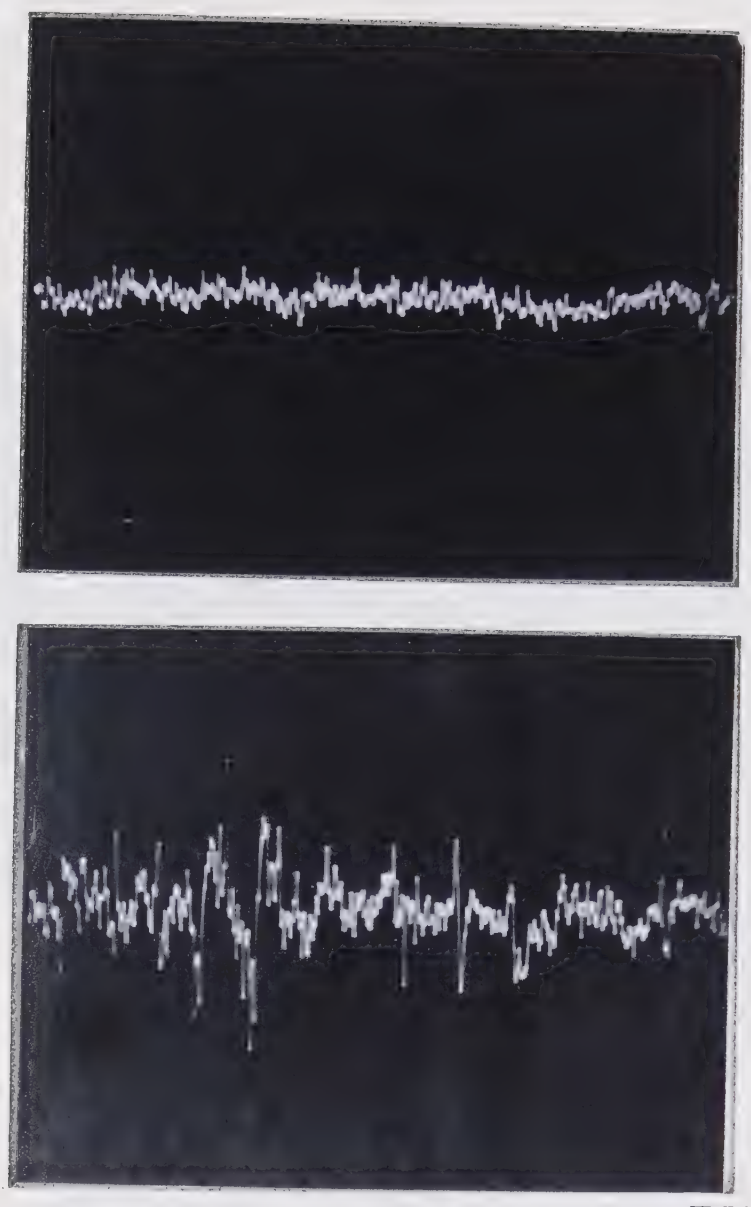


Figure 28. A. Top: Spontaneous Mes V activity.

Bottom: Mes V activity when mandible is depressed
to stretch jaw elevator muscles passively.

Vertical calibration: 0.08 mv.

Horizontal calibration: 20 msec.

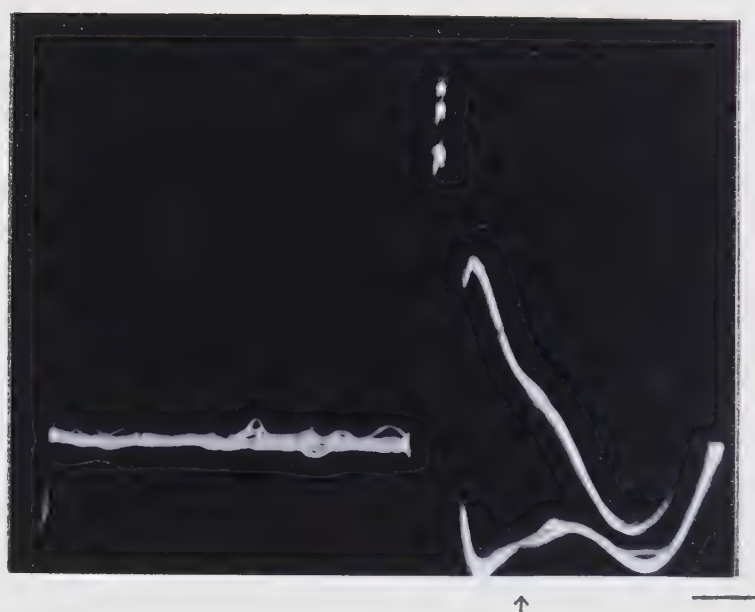


Figure 28. B. Electrical stimulation of Mes V spindle units, Rat 23. Ten superimposed traces, five with normal and five with reversed stimulus polarity. Stimulation is applied to spindle(s) in deep masseter.

Vertical calibration: 0.1 mv.
Horizontal calibration: 0.5 msec.

jaw elevator muscles.

The usual method of obtaining spindle activity in humans is the jaw jerk, quickly stretching the jaw elevators by a tap on the chin with a reflex hammer. Good practice requires placing the examiner's finger between chin and hammer. Such a procedure is impractical for the rat due to his small size, lack of a chin, and prominence of the lower incisors. The consequence of these anatomical details is that any attempt to administer the jaw jerk to a rat runs directly into the teeth. However, infiltration of as little as 0.2 ml of 1% lidocaine is sufficient to block the jaw opening response obtained from tapping a tooth, five minutes after application in dog and cat (Hannam and Matthews, 1968).

Figure 29 pictures such a jaw jerk performed on Rat 27. The animal was coming out of light pentobarbital anesthesia when the lower incisors were infiltrated with 2% lidocaine. After the lower lip was entirely without sensation (the animal could almost walk around at this stage), a triangular metal probe attached to a microphone was used to hit the lower incisors to approximate the jaw jerk. No jaw opening response to hitting the teeth occurred, so it seems likely that the periodontal receptors were non-functional. The top trace is the direct brain response, in the center is the integrated form, while the lower trace is the audio record which marks application of the stimulus. The brain electrode (though not the integrator, with an averaging interval of 10 msec) is responding with a latency of about 2 msec, the time normally required for natural (as opposed to electrical) stimulation

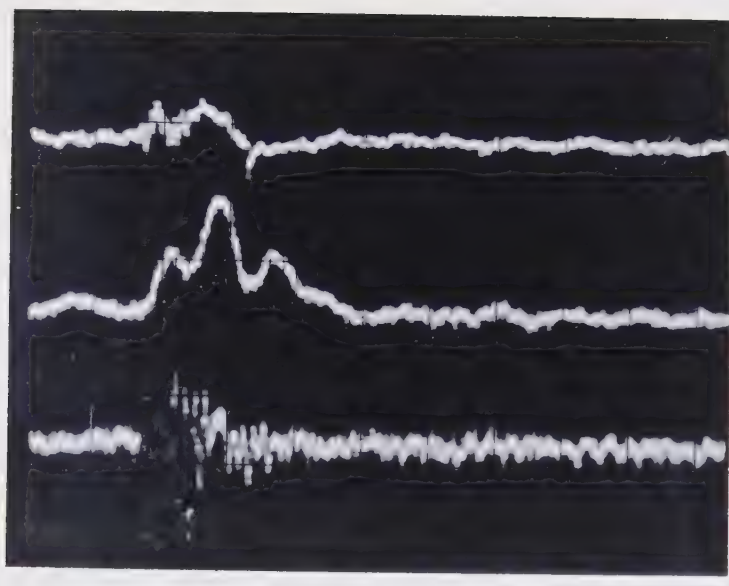


Figure 29. Rat 27: "Jaw Jerk".

Top: Mes V, vertical calibration = 0.53 mv

Middle: Integrated Mes V, vertical calibration = 0.11 mv

Bottom: Audio, vertical calibration = 0.05 v

Horizontal calibration = 20 msec

of a Ia cell to reach Mes V (Thomas, 1972). Unfortunately, it is nearly impossible to simply hit the teeth once with such an inelastic instrument as the edge of a triangular probe. So several peaks of activity are apparent in the picture. This response is probably less a jaw jerk or stretch reflex in the classic sense, however, than it is a response of the spindles to vibration. Similar results may be obtained by tapping the top of the snout or the forehead. And under those circumstances, tooth receptors would not be involved.

Small amplitude vibration of the muscle is used to differentiate Ia fibers from Ib or II (Brown, Engberg and Matthews, 1967). This was tried with the rat, both under pentobarbital and in the decerebrate animal. In Figure 30, the jaw is being stretched using pulses at 30 Hz and 0.6 mm amplitude. Pentobarbital was used. Note the on-off response to the pulse. Similarly, Figure 31 (decerebrate preparation) demonstrates driving of Mes V in response to A) 15 Hz pulses (jaw is briefly released from stretch at each pulse), and B) 100 Hz square wave with stretch of the muscle at the downward deflection of the transducer trace.

When an animal comes out of anesthesia, some interesting responses are observed. Figure 32 illustrates four responses in an animal emerging from pentobarbital anesthesia. The animal could move the head and could just begin to move the limbs as well. In trace B, the rat's molars are pressed tightly around a glass rod, placed in his mouth to ensure good tooth contact and therefore a maximal response from tooth receptors. In C, the mouth was stretched

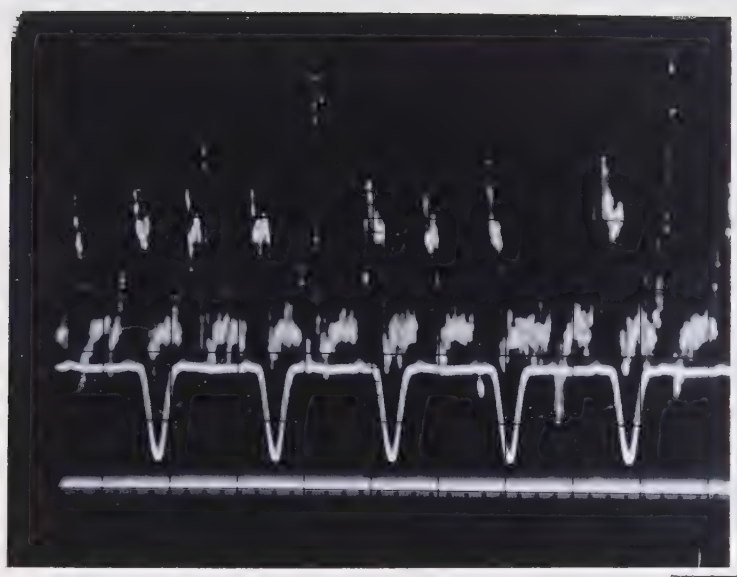


Figure 30. Top: Mes V response to 30 Hz jaw stretch, vertical calibration = 0.053 mv.

Bottom: Length transducer, vertical calibration = 2 v (0.6 mm) \downarrow stretch

Horizontal calibration = 20 msec

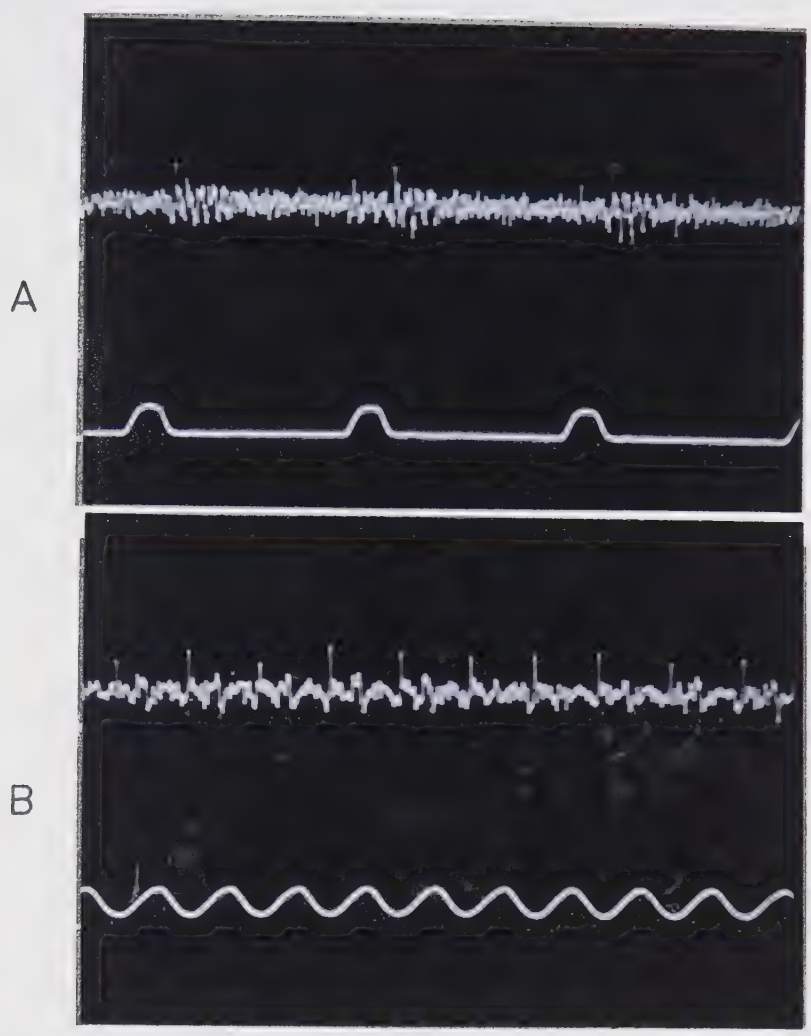


Figure 31. Mes V "driving" in the decerebrate rat.

A. Response to pulse stretch of jaw elevators at 15 Hz.

Top: Mes V, vertical calibration = 0.02 mv.

Bottom: Length transducer, vertical calibration = 1.0 v; ↓ stretch.

Horizontal calibration = 20 msec.

B. Response to square wave stretch of jaw elevators at 100 Hz.

Top: Mes V, vertical calibration = 0.02 mv.

Bottom: Length transducer, vertical calibration = 1.0 v; ↓ stretch.

Horizontal calibration = 10 msec.

Iv = 0.2 mm stretch.

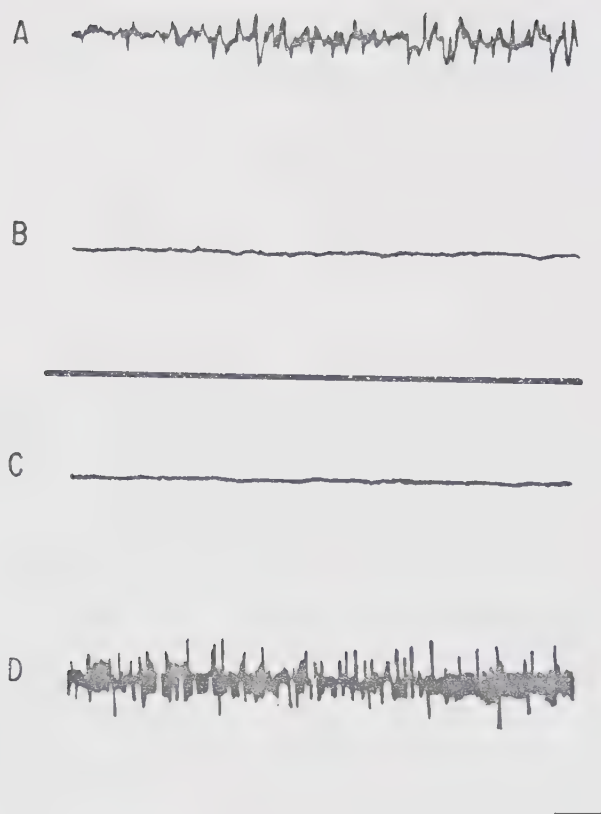


Figure 32. Test for Mes V receptor type in conscious rat - Rat 30.

- A. Animal actively chews on glass rod between the teeth.
- B. Molars are passively pressed against same glass rod.
- C. Mouth is stretched open - until subject jerks away.
- D. Animal actively tries to close mouth against load (experimenter is holding mouth open).

Horizontal calibration: A and B = 10 msec
C and D = 20 msec

Vertical calibration = 0.053 mv

open - until the animal jerked away - to obtain a spindle response to muscle stretch. Neither trace shows any activity. A shows the activity in Mes V as the rat *himself* chews on the glass rod. In D the animal tries to close his mouth against an imposed load (I am holding it open using snout and lower lip; teeth are not touched). Both A and D show considerable activity. Except for the difference in time base (calibration for A is 20 msec, that for D is 50 msec), the traces seem indistinguishable. Good "jaw jerk" and "vibration" responses to tapping on parts of the head were also obtained when the animal was coming out of pentobarbital anesthesia. They appeared to be the same as in the anesthetized rat.

Using the decerebrate preparation, Thomas (1972) found that spike amplitudes of Mes V spindle units are considerably larger than spike amplitudes of periodontal receptors. His finding was confirmed in this study.

All electrode positions were verified histologically (see *METHODS*). A typical electrode track is illustrated in Figure 33. Figure 34 shows the relative positions of all Mes V electrodes used in this study.



Figure 33. Typical electrode track: Rat 10.

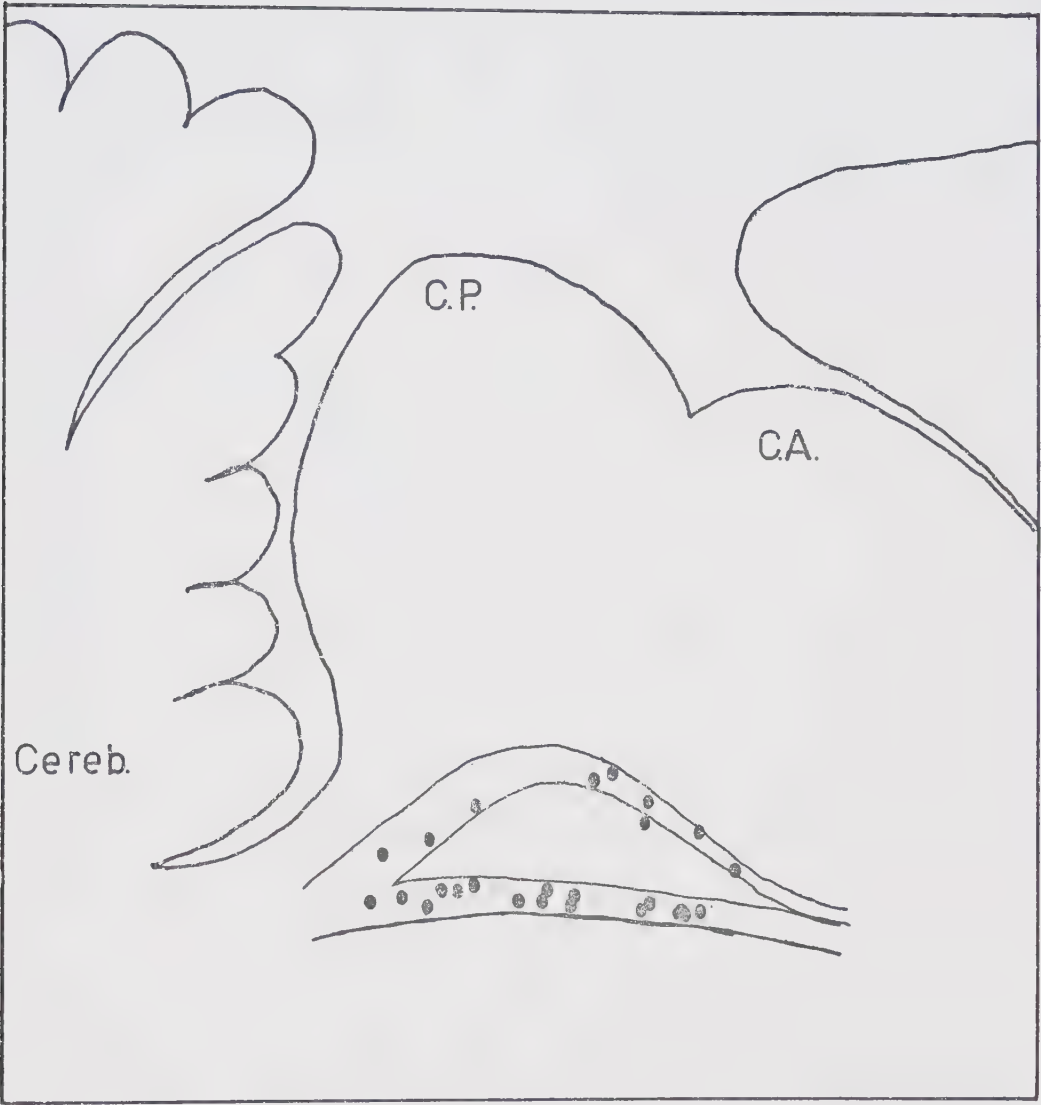


Figure 34. Position of Mes V electrodes used in this study.

VI. *DISCUSSION*

According to the reflex theory of mastication (Jerge, 1964; Sherrington, 1917), mandibular elevator muscle spindles must be active during the opening phase of chewing, when the jaw elevators are being stretched. Activity in Mes V during stretch of the jaw muscles was consistently found in anesthetized or decerebrate animals (Cooper, Daniel and Whitteridge, 1953; Corbin and Harrison, 1940; Jerge, 1963; Kawamura, Funakoshi and Tsukamoto, 1958; Smith and Marcarian, 1968; Thomas, 1970). Spindle activity during contraction was found by Davey and Taylor (1966, 1967; Taylor and Davey, 1968) using cats emerging from anesthesia. They stated that Mes V recording must be done on normal animals to resolve the issue. The results of the foregoing study indicate that muscle spindle activity occurs only during active contraction of the elevator muscles when a normal animal chews his food. If this observation is true, the reflex theory of mastication must be abandoned.

This interpretation might be challenged on a variety of grounds. However, steps were taken to verify results and to remove ambiguities regarding their significance. The interpretation is supported by the evidence summarized below.

Mes V activity, as measured by chronic multiunit electrodes in freely moving rats, occurs during the same time period as activity in two of the jaw elevators, masseter and temporalis. At this time, the jaw muscles are not lengthening, but the mouth has actually undergone some closure and the muscles are shortening. Activity is there-

fore increasing as the spindles are being unloaded. During observation of chewing in twenty-five animals, over several test sessions each of which consisted of well over 1,000 chewing cycles, no instance of Mes V activity during jaw opening was found.

Is the activity observed during closing due to spindles? Since cell bodies of tooth receptors and perhaps Golgi tendon organs are also found in Mes V, they could be responsible for the observed activity.

Use of small amplitude vibrations can be used to differentiate Ia, Ib and II fibers (Brown, Engberg and Matthews, 1967). It has been shown that discharges in units of Mes V would follow frequencies of 100 Hz at an amplitude of less than 0.2 mm. This may be Ia activity, but there are problems with such an interpretation.

Although secondary fibers probably were not involved (if, indeed, they are present in Mes V), it is known that Ib fibers become considerably more sensitive to vibration if the muscle is contracting when vibration is applied. Since it is not possible to separate afferent and efferent fibers in the masticatory muscles (as is done comparatively simply by dorsal or ventral root section for spinal nerves), vibration and the consequent activation of Ia fibers probably caused contraction in the elevator muscles. Therefore the sensitivity of Ib fibers to vibration would be increased (and sensitivity of Ia fibers somewhat decreased, due to unloading effects), making this test equivocal at best. Adding to the difficulty of interpretation is the presence of periodontal receptors in the system.

Since the connection to the jaw had to be made across the lower incisors, they could be activated also, even though the jaw and its connecting wire were under considerable maintained tension. Pfaffman (1939b) had shown that tooth receptors could follow vibration of up to 520 Hz for individual units or above 1,000 Hz for the inferior dental nerve.

It is still rather unlikely that Ib fibers constitute much of the Mes V activity seen in these records. As discussed above, the silent period represents tooth contact, at least in humans (Ahlgren and Öwall, 1970). It has been shown that maximal chewing force, and thus presumably maximum Ib activity, occurs after tooth contact is made (Ahlgren and Öwall, 1970) and outlasts the occlusal phase. That force lasts beyond the EMG activity of masseter in the rat was shown by increased jaw closure after that point in chewing of bread and large and small pellets. Therefore Ib activity should be found after the silent period and should last longer than activity in the jaw elevators. On the contrary, Mes V activity both precedes the masseter EMG, and thus the development of force, and also ceases either with the end of masseter EMG or even sooner, while force is still being exerted.

Both tooth receptors and muscle spindles are represented in Mes V. Spindles represented 78% of the cells found by Jerge in Mes V (1963a; no Golgi tendon organ cells were found) and 65% of the cells found by Smith and Marcarian (1967). Tooth receptors comprised 22% and 29%, respectively. No comparable study has been done for the rat.

Work reported here confirms the earlier study of Thomas (1972)

which found that the relative amplitude of spikes from Mes V spindle cells was several times larger than that from tooth receptor cells. In fact, response of the latter is quite close to background levels of activity normally present. Ness (1954) found both fast- and slow-adapting tooth receptors in the rabbit. Jerge (1963a) using cat, believed that most of the Mes V tooth receptors were rapidly adapting. Again, no comparable study exists for rat. Slowly-adapting cells in rabbit fire as long as pressure is applied to the tooth. Therefore they should continue firing as long as force is being exerted between the teeth. This lasts beyond the EMG, as discussed above, so this receptor also should be active longer than the period of Mes V activity shown here. If, on the other hand, rapidly-adapting tooth receptors are present, they should fire at make and break of tooth contact. No such activity is seen on break of contact, though of course "make" would quite easily be lost in spindle activity. Perhaps both are present, but too small to greatly influence the gross pattern of activity.

Do these electrodes record activity from spindles? Passive stretch of the jaw elevators produces an increase in Mes V activity. Using localization by probing with a fine glass rod or, more often, a wooden probe (as Matthews, 1933, among others), specific spindles have been localized. Electrical stimulation was then used to determine latency; this was found to be in the 0.5 to 0.8 msec range for direct activation of Mes V spindle units. Vibration responses have been recorded in Mes V not only from the "jaw jerk" (obtained by tapping the lower incisors, since the rat "chin" is actually the upward curve of these teeth), but also from tapping snout or head. Tooth response was eliminated by

infiltration of lidocaine, and the response did not change in form.

All of the above were done on anesthetized or decerebrate animals. However, as an animal emerges from anesthesia and becomes able to control his head, it has been shown that similar strong responses are recorded by these electrodes both as the animal chews on a glass rod and as the animal tries to close his mouth when it is being held open. The two responses were difficult to distinguish from each other in any important respect, although tooth receptors could not have been activated in the latter case. Neither pressing the teeth passively around the glass rod nor forcibly depressing the mandible to stretch the jaw elevators produced any response. However the animal would jerk his head before these muscles were stretched very much. Therefore in the conscious rat, responses registered by the chronic Mes V electrode appear to be due to response of muscle receptors rather than to tooth receptors.

It would appear from the above that the conclusion stands: Muscle spindle activity occurs during active contraction of the elevator muscles when a normal animal chews his food.

In addition to the work on the relation of activity in Mes V to the chewing process, this study has included a description of the muscle activity and jaw position during active chewing for several types of food. No similar animal study is known to the author.

The variability among animals is illustrated by differences in duration of masseter activity when eating a large pellet.

Although Rats 9, 19 and 32 all chewed this hard food at about 5.4 Hz (cycle times 185, 180 and 187 msec), the duration of activity varied considerably (77, 98.5 and 38 msec). Similar differences were true for other parameters. Nevertheless, some general observations are justified.

The basic findings of Hiemäe were confirmed in this study. Incision of hard food required several rapid chopping strokes to break off a piece. A soft food like pudding is sucked into the mouth. Normal molarization involves from 25 to 35 cycles. It is believed that the "aberrant" form of digastric activity pictured in Figure 24 may correspond to swallowing, since it appears three times during such a period of molarization and Hiemäe found that three boluses were swallowed during such a period. Superficial masseter was supposed to effect the gross protraction needed for incision. A very small amount of masseter EMG or Mes V activity is seen during incision, corresponding both to the small size of this division of the large masseter muscle and to the small number of spindles (six) found in it by Karlsen (1965). Hiemäe believed that deep masseter would be involved in the actual "power stroke" of incision, however, and this seems less likely.

Basic chewing rates were similar for large and small pellets (5 to 5.5 Hz), while bread was faster (6.3 to 6.4 Hz) and pudding much faster (10 Hz). Cycle time appears to vary with load, the harder food requiring the longer cycle time. Closing and occlusion periods were quite brief for both kinds of pellet while opening lasted over 70% of the cycle. For bread, however, opening

and closing were both about 40%; that is, the opening phase was shorter and closing longer.

Temporalis and masseter act together on incision, but temporalis is activated before masseter in molarization. During incision, masseter amplitude is greatly decreased, while duration is lengthened. (Activity in digastric is almost continuous during incision.) Neither masseter nor temporalis display "secondary activity". This agrees with Møller's findings in humans (1966). Møller found that internal pterygoid was the first jaw elevator to be activated. It would be interesting, though extremely difficult, to try to confirm this for the rat.

Two periods of activity per cycle were found for digastric. This was always true. There is a real possibility that these electrodes were picking up signals from the more powerful contractions of masseter. This was a definite problem in cat EMG studies (Yemm, personal communication) and may be occurring here. This seems plausible since often the secondary activity seems to be larger than the primary and in general, signal sizes in masseter for this animal were three to four times larger than those recorded for digastric activity.

Against this argument are the numerous cycles in which masseter activity was quite high while that in digastric was low, that the Pearson correlation coefficient relating secondary digastric and masseter EMG amplitudes was not significant, that usually individual bursts of activity shown in the filtered trace were similarly variable, and the fact that in most animals masseter activity started clearly in advance of that in digastric. Møller's study of human chewing (1966) reported that digastric was

activated at the time of maximal activity in temporalis, his reference muscle, which is also the time of tooth contact. Mylohyoid was activated even sooner. He considered these activations to be the primary activity of the muscle since they had their maximal amplitudes when activity was no longer evident in temporalis. In fact, they looked very much like the aberrant digastric cycle of Figure 24. However, this is very probably activity associated with swallowing a bolus. In addition, Møller found both digastric and mylohyoid almost continuously active between the long periods of primary activity, especially in natural chewing (as opposed to chewing gum). The third jaw opener studied by Møller, lateral pterygoid, was more similar to the usual pattern found in rat digastric than were either human mylohyoid or human digastric. The opening or primary activity occurred in the quiet period between bursts in temporalis, while the secondary activity was found occurring at just about the same time that temporalis was active.

A silent period is seen in masseter, temporalis and Mes V records. Its timing appears to coincide with tooth contact, though this cannot be certainly determined from this study. Silent periods of human masseter and temporalis have been extensively studied by Hannam and Matthews and Yemm (1969, 1970). These periods follow mechanical tapping of a tooth. However, local anesthesia around the teeth does not eliminate the response. The same response was produced by a "jaw jerk" or vibrating the skull as the subject contracted his jaw elevators by biting on a bung. It is felt that the silent period follows the response of muscle spindles to vibration.

The spindles fire synchronously due to the vibration stimulus of tooth contact, causing the muscle fibers to contract reflexly; the silent period which follows is the refractory period for spindles and muscle fibers, not usually observable since the normal discharge pattern for both is asynchronous. Tooth receptors may play some part in this also, according to a recent paper by Goldberg (1971).

The results of this study indicate that since muscle spindles fire during active contraction of the jaw elevator muscles, the reflex theory of mastication is incorrect. Instead, chewing seems to be under some form of central control which uses alpha-gamma coactivation as the basic regulatory mechanism. Thus chewing, like walking and breathing, is not controlled by an alternation of simple reflexes. Instead, these reflexes probably serve to modify a basic pattern. Is this pattern some form of oscillator, as suggested for breathing and walking? Experiments on the decerebrate rat produced chewing which was remarkably similar to that found in the normal animal. Mes V activity occurred with contraction of jaw elevators in this case also. The main difference was the amazing degree of regularity seen in Mes V, masseter and digastric patterns when compared to the normal animal. These experiments suggest that the midbrain region is the location of this oscillator.

Perhaps most research raises more questions than it answers. This study is no exception. Clearly it is necessary to learn much more about the rat before the information obtained here can be explained fully. Mes V needs to be mapped for presence of spindles, afferent tooth receptors or Golgi tendon organ cells. Single units should be studied during active chewing sufficiently to correlate unit responses with the multiunit activity of this study. Although the EMG electrodes used were ideal for an overall view of muscle activity, finer electrodes would be useful for further work. For instance, digastric and mylohyoid muscles are very small in a rat. Even if masseter was not influencing my digastric records appreciably, the small mylohyoid muscle may have been. (Like digastric, mylohyoid is a jaw opener, and in humans mylohyoid activity closely parallels that of digastric. Any influence from it in the digastric trace would not change the basic conclusions of the study.) What are the functions of anterior as compared to posterior temporalis, or deep masseter compared to superficial? How are muscles on right and left sides related in the normal chewing of a rat? Where in the midbrain is the central oscillator and what is its probable structure? The research has only begun.

VII. CONCLUSIONS

1. A head assembly is described to record Mes V and EMG activity simultaneously in the rat while he eats his normal food. The assembly may be worn by the animal for several months without apparent discomfort.
2. Mes V, temporalis, and masseter are active only during the closing phase of the chewing cycle. The digastric muscle is active twice in each cycle, not only during the opening phase but also during the closing phase, concurrent with Mes V and the jaw elevators.
3. Normal molarization involves from 25 to 35 cycles. As in humans, cycle times vary with load, so that chewing pellets is slower than chewing bread which is slower than eating pudding.
4. Closing and occlusion periods were very short when the animal ate either large or small pellets, while opening lasted over 70% of the cycle. Opening and closing phases lasted 40% of the cycle each when the animal chewed bread.
5. A silent period was seen in Mes V, temporalis, and masseter.
6. All Mes V activity recorded occurred during jaw closure. These bursts were found to be largely composed of muscle spindle activity. Thus spindles were active only while the muscles were being unloaded. Since the reflex theory of mastication requires spindle activity when the jaw elevator muscles are stretched, the reflex theory of mastication is disconfirmed.

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APPENDIX

A. Use of Multiunit Electrodes

In a variety of studies, close correspondence is reported between multiple unit activity and single unit experiments (Buchwald *et al.*, 1969; Podvoll and Goodman, 1967; Schlag and Balvin, 1963; Starr and Livingston, 1963; Winters *et al.*, 1967). This multiunit activity cannot be equated with the behaviour of a single discharging neuron, although it does represent primarily action potential discharge of cells and fibers around the recording electrode. The activity seen is complicated by possible fast EEG components, complex wave forms of the recorded action potentials, summation of rapidly discharging potentials, and differentiation of the activity by the high pass filter. It provides a "summary of the resultant activity at the recording site based primarily upon local action potentials" (Buchwald *et al.*, 1969). The advantage of the technique is that it removes some of the population bias and also some of the practical difficulties of single unit studies. For this reason it is used preferentially in studies on chronic freely moving animals (Buchwald *et al.*, 1969; Schlag and Balvin, 1963). The basic method was developed by Arduini and Pinneo (1961).

The usual method uses insulated stainless steel wire electrodes with tip diameters of 20 to 80 μ and resistance of 30 to 50 K Ω or somewhat higher, depending on the author. Electrodes of similar resistance should be used in a given preparation. After passing through a bandpass preamplifier (common ranges are 250 to

2,500 Hz, 300 to 3,000 Hz) used particularly to limit low frequency components, the activity is usually full wave rectified and fed into an RC integrator circuit or, sometimes, into equipment that directly presents frequency changes rather than the amplitude changes shown by the integrator. There is close correspondence between experimental results obtained by these two methods (Buchta, 1969). Monopolar recording is preferred due to the greater accuracy in determining origin of the observed potentials. The amplitude sensitive systems are, of course, more easily influenced by changes in firing rate of cells having large amplitude unit spikes. Small amplitude cell frequency changes can easily be lost. Therefore the sample is definitely biased toward frequency changes in cells having the larger action potentials. Also, simultaneous positive and negative spikes would cancel each other (Schlag and Balvin, 1963).

B. *EMG Electrodes*

Both Møller (1966) and Ahlgren (1966) performed fairly extensive tests on electrode types and characteristics before proceeding with their studies. Møller used surface electrodes on masseter and temporalis. He found that their surface EMGs contained frequencies of at most 600 Hz; these were extremely few. The frequency distribution had its peak at from 100 to 200 Hz. Møller found that for a bipolar interelectrode distance which is small compared to the size of the muscle, conducted activity from nearby muscles is almost identical on the two leads and therefore is

rejected. Concentric needle electrodes were used for the pterygoids, mylohyoid and digastric due to the mechanical difficulties of reaching them with anything else.

In Ahlgren's study, it was found that platinum wire electrodes (0.18 mm) with the end bent into a 5 mm hook and placed beneath the skin caused little discomfort to the subject once they were in place. These electrodes "picked up motor unit potentials as accurately as concentric needle electrodes and displayed the activity of a whole muscle as efficiently as bipolar surface electrodes". They were more reliable in picking up activity from the specific muscle being studied than are surface electrodes. Needle electrodes changed position during recording of active chewing.

The well-known work on walking in unrestrained cats by Engberg and Lundberg (1969) used electrodes rather similar to those of Ahlgren. They were made of 0.1 mm enamelled copper wire, bent into a hook at the end and having about 1 mm of the insulation removed from that hook. The electrodes were inserted within a hypodermic needle which was then withdrawn. Electrodes were removed after each experiment. Animals wore light-weight transmitters and therefore were entirely free of wires. Only one muscle was recorded from at a time. Both the direct EMG and the signal integrated by an RC network after full wave rectification were used to analyse the movements. Relative limb movements were obtained by photographing the cat with flashes of light at 100 to 200/sec.

The electrodes used in this study are very similar to

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The electrodes used in this study are very similar to

those utilized by Ahlgren and Lundberg. However, instead of a hook, movement of the electrode in the muscle was prevented by taking a small stitch of about 1 mm into the muscle and wrapping the end once around the insulated standing part of the electrode. This resulted in a small loop and thus a slightly greater exposed surface. However, these bipolar electrodes (since they were placed in pairs having an interelectrode distance of about 1 to 2 mm) could remain in position for several months.

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